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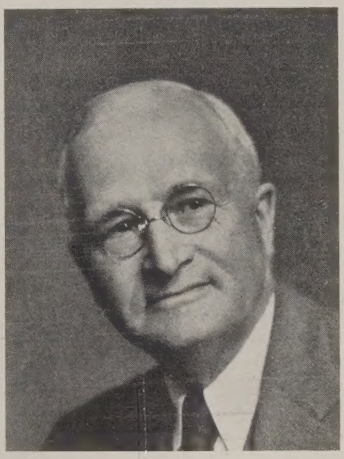
FREDERICK CHARLES ELFORD—AN APPRECIATION

GEO. ROBERTSON[1]

Central Experimental Farm, Ottawa, Canada.

This issue of *Scientific Agriculture* is devoted especially to poultry research carried on by workers of the Poultry Division of the Experimental Farm. It therefore appears appropriate at this time to present an appreciation of the man under whose guidance this work has been carried out, and more especially since he is about to sever his connection with the Division to take up duties for which he is so eminently fitted.



Frederick C. Elford was born at Crosshill, Waterloo County, Ontario, on June 29, 1871, the son of Herbert and Mary Elford. When he was two years of age the family moved to Huron County. The father, a thrifty, hard working and efficient farmer was rather a strict disciplinarian, and in this rugged atmosphere young Elford received his early training. He was educated at the Holmesville Public School, the Clinton Collegiate Institute, and the Ontario Agricultural College, after which in 1893 he took up general farming at Holmesville, Ontario. In 1896 he married Ellen, daughter of A. J. and Mrs. Courtice of that place. During this period he did consideraable lecturing for the Farmers Institutes of Ontario. It was during this time that the late Dr. Jas. Robertson, at that time Commissioner of Agriculture for Canada, decided to start poultry fattening stations in different sections of Canada. Dr. Robertson selected Mr. Elford as a suitable manager and opened a station on his farm at Holmesville. This he operated from 1901 to 1904 when he was called to Ottawa for the more important position of Chief of the Poultry Division of the Live Stock Branch. This position he filled until 1906 when he resigned to go to Ste. Anne de Bellevue to assist Dr. Robertson in establishing the Poultry Department at Macdonald College, where he remained as manager and lecturer until January 1, 1912. He then resigned this position to enter commercial life with the Cyphers Incubator Company of Buffalo, N.Y., remaining only until July 1st when he returned to Toronto as Canadian representative of the Candee Incubator Company.

[1] Assistant Dominion Poultry Husbandman.

About this time Dr. J. H. Grisdale, then Director of the Experimental Farms, was scanning the field of poultry workers in order to find a man suitable to replace the late A. G. Gilbert who was in charge of the poultry work at the Central Farm and who had reached an age when he wished to take a well earned rest. It was also desired to extend this service, making a Division which would include all poultry work over the whole Farm System from coast to coast. After a careful survey F. C. Elford was appointed first Dominion Poultry Husbandman in 1913, in which position he has continued until 1937.

The writer first became acquainted with Mr. Elford while attending the Ontario Agricultural College at Guelph in 1893 and this acquaintance was renewed when Mr. Elford came to Ottawa as Chief of the Poultry Division of the Live Stock Branch in 1904. A close intimate association has been maintained ever since. When F. C. Elford became President of the Poultry Producers Association of Canada, an association which he organized and fostered, the writer took over the duties of secretary, and in February, 1914 became Assistant Poultry Husbandman. He therefore feels that he perhaps knew more than anyone else of F. C. Elford's aims and aspirations for the industry, two of which might be mentioned:—

1.To convince the farmers of Canada that poultry keeping could be made one of the most profitable branches of agriculture.

2. To establish poultry keeping on a higher plane and to have it recognized and respected equally with any other branch of agriculture.

How well he has succeeded may be determined in part from the following figures. At the time F. C. Elford became Dominion Poultry Husbandman poultry keeping was decidedly a small side line on the farms of Canada. In 1911, the nearest year in which census figures are available, there were less than 32 million head of poultry in this country; by 1931 there were 65½ million. In 1921 the first year for which census values are obtainable the crop was valued at slightly over 31 millions of dollars, whereas in 1929, the peak, the value of the poultry crop was over 62½ millions of dollars.

How did the Farms under Mr. Elford's guidance assist in this tremendous development? First, by demonstrations on the Farms to show the profitable returns that could be obtained, and second, by the distribution from the Central and Branch Farms of thousands of head of high production poultry among the farmers of Canada.

When the first egg-laying contest in America was established at Victoria, B.C., Mr. Elford was quick to perceive what a force this could be made in creating interest in the breeding of high egg-producing lines of poultry. In the fall of 1918 a laying contest was started at Charlottetown, P.E.I. This was an unqualified success. The following year the Canadian National Egg Laying Contest was established, adding, to the one already at Charlottetown, contests at Nappan, N.S., Cap Rouge, Que., Ottawa, Ont., Brandon, Man., Indian Head, Sask. and Lethbridge, Alta., later increased to 14 contests located from coast to coast. In 1920, Mr. Elford selected A. G. Taylor, who had formerly been associated with him at Macdonald College, to come to Ottawa to take charge of this part of the work, and a system of Registration was inaugurated whereby all birds

that conformed to the Standard and that qualified in the contests by laying 200 eggs in the contest year were recorded. Later, the qualifications were made more strict by requiring that the eggs laid must average at least 24 ounces to the dozen, and this had a great effect in stimulating breeding for egg production.

As to the establishing of the industry on a higher plane, the mere fact of a tremendously increased growth and value has contributed to this end. In 1924 the Hon. Mr. Motherwell then Minister of Agriculture, sent Mr. Elford to Barcelona, Spain, to the World's Poultry Congress, with an invitation from Canada to the Poultry Science Association to hold their next Congress at Ottawa, Canada, in 1927. This invitation through the persuasive powers of Mr. Elford was accepted and the Congress at Ottawa was carried out under his direction on such a scale and with such pomp and ceremony as to impress not only the general public but governments and financial interests with a sense of the importance of the industry such as had not previously existed.

In more recent years the work at the Farms has been gradually changing, fundamental research assuming a much more prominent part. In keeping with this Mr. Elford has gathered about him a group of young enthusiastic workers who are helping to solve the problems of the industry, as may be seen from the papers that follow in this issue.

So, through all his tenure of office, as twice president of the American Poultry Science Association; president of the Ottawa Poultry Association; Director of the 1927 World's Poultry Congress; president of the World's Poultry Science Association, (when in the interest of that Association he visited all but two of the countries of Europe, Egypt, Palestine and Turkey and interviewed their Governments); Presiding officer of the 1930 World's Poultry Congress in London, when it was his duty to reply to the address of welcome by the Duke of York, now King George VI; Canada's representative at the succeeding World's Congress held in Italy in 1933 and Germany in 1936; President of the Ottawa Rotary Club and recommended by Ottawa Rotary as Governor of International Rotary; and Director and Vice-President of the Central Canada Exhibition, he has ever striven to dignify and elevate the industry of which he is justly proud. And now when he is leaving his task for someone else to take up, instead of taking the rest which he has so well earned, he is taking up a task, not so onerous perhaps, but one which carries heavy responsibilities and honour such as he deserves—Special Commissioner, loaned by the Canadian Government to our friendly neighbours in the United States, at their request, to assist with his vast experience and sane council in helping to carry to a successful conclusion the World's Poultry Congress of 1939 which will undoubtedly be the greatest the World has ever seen.

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METHODS AND RATIONS FOR FATTENING POULTRY[1]

H. S. GUTTERIDGE[2]

Central Experimental Farm, Ottawa.

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INTRODUCTION

There is perhaps no phase of poultry husbandry which has received as little attention from a research standpoint as that of fattening for market. The reasons for such a condition are fairly obvious. Of most importance in this connection is the fact that table poultry is, to a large extent, merely a by-product of poultry keeping for the production of eggs. Demand has also been an important factor, since the hen's egg is practically without competition from products of other species, whereas the available meats upon the market are many and varied. Under the circumstances the demand for, and consequently the production of, table poultry of really high quality has been limited, being confined mostly to the larger cities and being seasonal in nature even to the extent of being a holiday or festive season demand. Of recent years however, the public has gradually become somewhat more conscious of the importance of quality in dressed poultry, and an increasingly larger percentage of consumers attach as much importance to a well finished dressed chicken as they have always in the past attached to a loin cut of beef as opposed to the cheaper cuts. The reason for lack of interest in quality of poultry is therefore evident. Lacking the demand little attention was paid to the methods by which quality could be produced.

The chief underlying causes for lack of quality in dressed poultry are disease, improper feeding, and poor type. Of these, disease and improper feeding are of the greatest significance. Generally speaking it is not possible to market diseased poultry in good flesh or well fattened. Similarly poorly fed birds cannot be in good flesh or in fat condition. A bird of poor type, if free from disease, can be much improved by proper feeding during growth and by crate fattening at maturity. It is within the scope of this publication to deal only with the one factor, feeding, and under this heading only with that part of feeding just prior to marketing. The aim of this finishing period is generally considered to be to increase the weight of the bird, to soften the muscles, and to add as much fat as possible. This end is usually gained by crate fattening, and this treatment is of great importance chiefly because it contributes more to the market quality of the bird than any other feeding practice. As previously indicated, very few controlled fattening experiments have been carried out in the past, the technique which has grown up being mainly the result of practical experience and judgment. The research reported herein was carried out as a contribution to the existing knowledge of quality in dressed poultry and to the understanding of the effect of certain feeds and treatments upon that quality.

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[1] Contribution from the Division of Poultry Husbandry.

[2] Poultry Husbandman.

I. FATTENING TRIALS

Two fattening trials were undertaken during the fall and winter of 1935–36 involving in all ten feeding treatments and one matter of feeding technique. These trials will be here reported in detail together with notes upon the technique employed.

A. Technique

In this instance the technique employed in these trials covers the planning of the trials upon a statistical basis, the actual technique of feeding and management, the sampling of tissues for chemical analysis, and the chemical analysis itself. These techniques will be considered separately.

1. *Allotment*

For these trials a three-deck commercial laying battery was used as it was necessary to have individual feed data in order to be able to analyse thoroughly the information obtained. In order that all groups should have comparable conditions of environment, the birds were allotted at random to the different compartments and cages of the battery and to the different diets given. Since one factor, initial body weight, is definitely correlated with weight gain, the randomization was restricted by body weight as was done by Titus and Harshaw (1935) so as to equalize this factor as much as possible between groups.

2. *Feeding and Management*

After allotment all birds were starved for 24 hours with water to drink. At the end of this time they were weighed and the first feed given. Epsom salts at the rate of one pound per 100 birds was given with the first feeding. Limestone grit was also supplied at that time. Except where otherwise specifically noted two feedings daily were given. Sour skim milk was used as a mixer, the quantity being adjusted so as to give a mixed mash of similar consistency to all groups. Also, except when otherwise noted, the feed was left before the birds for one-half hour. It was actually found that all birds had ceased eating at the end of that time. All feed was carefully weighed out in grams and the unconsumed residue weighed back. The feeding hours were 7.30 a.m. and 4.30 p.m. daily. In addition to the individual weighings of birds at the commencement of the test, weights were taken each seventh morning with an additional final weighing on the morning of the twenty-second day of the test after twenty-four hours of starvation. Thus the gain in body weight calculated for the experiment represents the difference between the first and final starved weights.

3. *Sampling*

Since fat determinations of various portions of the carcass were desired appropriate samples from the birds to be analysed were taken. Samples for determination of percentage fat in breast muscle, for percentage fat in skin and subcutaneous tissues, and for percentage fat in abdominal tissue were required. It was determined by making chemical analyses that the percentage fat of the breast and of the skin and subcutaneous tissues for the two sides of the same bird checked very closely. For these samples therefore, only the left side of each bird was used. The skin of the birds

(which was stored frozen pending sampling) was slit upon the median line longitudinally around the bird with scissors and the skin of the left side removed with all adhering subcutaneous fat leaving only upon the carcass that skin which was above the ear lobe. Since in this process only a small proportion of the total subcutaneous fat was removed with the skin, the remaining subcutaneous fat was all dissected off the surfaces to which it adhered and included in the skin sample. The subcutaneous fat upon the breast was taken with the skin since being but loosely attached to the breast surface it obviously represents a depot of fat which cannot be said to be a part of breast tissue.

The breast sample was taken by dissecting out the prectoralis major and minor muscles in entirety, the small leaf of depot fat between these muscles in the region of the anterior attachment of the muscles being neglected.

In sampling abdominal fat, all free fat in the abdominal cavity was removed. The fat was also stripped from the gizzard and proventriculus. The intestines and mesentery were then removed completely, the gut slit from end to end, rinsed thoroughly with cold water to remove all adhering intestinal contents, allowed to drain for ten minutes and added to the other abdominal fat already removed. Since a great deal of fat is deposited upon the surface of the gut as well as in the mesenteries these portions must logically be included in any sample of abdominal fat. The three samples taken were then weighed separately in Erlenmeyer flasks and chemically analysed.

It should be emphasized that great care was taken to sample all birds in an identical manner.

4. *Chemical Analyses*

The fat was determined gravimetrically on HCl digests of large samples of tissue extracted with diethyl ether in a Friedrichs type of extractor.

From preliminary trials it appeared that an accurate determination of the fat by analysis of small (5–10 g.) samples by the method described by Holcomb and Maw (8) would be possible only with much more careful mixing of the minced tissue than was possible under our conditions. It was decided, therefore, to use all the tissue from one side of the bird (in the case of skin and pectoral muscle) and all of the visceral fat. The samples were dissected from the bird and weighed by difference as already described. A volume of conc. HCl approximately equivalent to the weight of tissue was added to each flask and the tissue digested for about 6 hours at 100° C.

Extraction chambers were made by fusing a side arm onto 800 ml. Kjeldahl digestion flasks. The hot HCl digests were transferred to the extraction chambers, washing first with hot water and, after cooling, with ether. Extraction with ether was continued for 18 hours, with the hot plate set sufficiently high to give a rapid flow of ether. It was found that most of the fat was extracted in 5 hours. Extraction was not complete at the end of 18 hours, but the amount of fat left was negligible when working with such large samples. This is illustrated by the following data.

Total fat obtained during extraction.

Tissue	Weight	18 hours		38 hours		58 hours	
	(g.)	(g.)	(%)	(g.)	(%)	(g.)	(%)
Skin (1)	107.3	35.631	33.21	35.686	33.26	35.714	33.28
Skin (2)	104.9	33.739	32.16	33.855	32.27	33.902	32.32
Abdominal	51.0	45.911	90.02			46.101	90.39

5. *Biometrical Analysis*

The method of biometrical analysis of the fat percentage data obtained from these experiments is set forth in Part II of this publication. The analysis of data for weight gain and for feed consumption was almost identical to methods set forth in a previous publication (Gutteridge, 5). In this instance the two factors of most importance which would affect the weight gains would be initial weight, previously referred to, and level of feed consumption. Obviously the larger birds would be expected to lay down a greater actual amount of new tissue and they also would consume more feed. These two factors, therefore, would be expected to have an influence upon the actual gains made even if groups were upon the same feed. Ideally, birds upon a feeding trial should all start with the same body weight and consume the same amount of feed in order to give an unbiased picture of the value of the feed given. Such equality is impracticable in actual tests. Consequently the weight gains obtained in this test were adjusted for the effect of varying initial weight and for that of varying feed consumption by statistical treatment of the data thus reducing the weight gains to those which would be expected had initial weight and feed consumption been the same in each group.

B. White Leghorn Capons

1. *Experimental*

The birds used in this series of tests were Single Comb White Leghorn Capons from 4.5 to 5.5 months of age and close to maturity at the commencement of the test. From a large flock, 140 individuals were selected upon the basis of apparent physical condition and body weight. All slips were discarded. During the allotment of these birds to positions in the battery every fifth bird allotted was retained for pen fattening. Consequently this pen group was strictly comparable to the other groups which were crate fattened. The mash used, unless otherwise stated, was composed of two parts of ground heavy oats to one part of ground barley. The following treatment was accorded to the different groups:—

Group A.—Dry mash and skim milk before the birds at all times.

Group B.—Wet mash composed of two parts of skim milk to one part of mash—*pen fed*.

Group C.—Ground raw potatoes in wet mash, equal parts of potatoes and mash by weight, mixed with one part of skim milk to one part of the mash potato mixture.

Group D.—Restricted feeding—wet mash composed of two parts of skim milk to one part of mash.

Group E.—Control—wet mash composed of two parts of skim milk to one part of mash.

Restriction of food for group D was accomplished by calculating the amount of food to be given on the basis of the surface area of each bird by the formula suggested by Mitchell *et al.* (10) and at a level of 85% of expected consumption as determined from an analysis of previous fattening data.

2. *Results*

The results obtained are set forth in Table I.

TABLE 1.—ACTUAL WEIGHT GAIN, ADJUSTED WEIGHTED GAIN AND CONSUMPTION OF DRY MATTER FOR ALL GROUPS

Group	Actual gain	Adjusted gain	Consumption Dry matter
	gms.	gms.	gms.
A.—Dry mash + milk	315.2 ± 20.3	335.5 ± 13.44	2872.9 ± 60.4
B.—Pen fed, wet mash	300.4 ± 27.1	– –	2699.1 –
C.—Raw potatoes + mash	391.5 ± 24.8	403.5 ± 14.03	2903.6 ± 65.6
D.—Restricted feeding	445.7 ± 22.4	439.8 ± 13.18	2976.1 ± 68.4
E.—Wet mash (Control)	452.6 ± 22.8	428.9 ± 13.18	3070.1 ± 78.7

3. *Discussion*

In considering actual gain it will be noticed that dry mash plus milk to drink, before the birds at all times, was definitely inferior to the ordinary fattening treatment accorded to the control pen (Pen E), the difference being 35.8%. It will also be noted that they consumed somewhat less dry matter although their actual consumption of milk was considerably greater than that of the other pens. It seems apparent that this additional consumption of dry matter of milk had little if any effect in enhancing weight gains. It is also particularly noticeable that the pen-fed birds were very low in weight gains (40.4% lower than the control group) a fact which is reflected in the very low feed consumption. This very low consumption of the identical feed which the capons in the battery found to be quite palatable is difficult to explain as it was observed that competition at the troughs was not particularly keen. The pen birds appeared to be much less keen for food at feeding time than did those being crate fattened. In view of the precautions of allotment of birds and similarity of treatment in every respect excepting the penned condition in lieu of the battery cage, it must be concluded that this environmental factor (pen) was mainly responsible for the result obtained.

A consideration of the weight gained by the birds on raw potatoes indicates this method of feeding to have been somewhat inferior to the restricted feeding group (control mash) although being definitely superior to the dry mash plus milk and pen feeding treatments. It will be observed in referring to the rations given that this group (potatoes) received only one part of skim milk to one part of mash (by weight) whereas the other groups received twice this amount. It is impossible to measure the effect of this slightly lower consumption of dry matter of milk, although in view of the apparently limited effect of the increased milk to the dry mash fed pen the possibility of this reduced milk intake being of any importance is questionable.

When the chance differences in body weight and feed consumption are taken into consideration and the weight gain adjusted to that gain which is freed of these influences, the "adjusted gain" of the table is obtained. It is apparent from these figures that all other treatments were definitely superior to the dry mash + skim milk to drink treatment. The group on restricted feeding treatment was also superior to the raw potato fed group (8.6% difference). There was no significant difference between the control and restricted feeding pen. It should be noted that it was found impossible to satisfactorily restrict the feeding to a definite percentage of expected consumption owing to the very great difference in consumption of some birds of similar surface areas, and of the same bird from day to day. What restriction was accomplished, however, was not detrimental to the gains made.

4. *Summary*

The data presented indicate that the feeding of wet mash, mixed with skim milk at the rate of two parts of milk to one of mash, for one-half hour periods, twice daily, to Leghorn capons in fattening crates gave definitely superior weight gains to those obtained by the following treatments:—

1. The feeding of the same mash dry with milk to drink, both being continuously before the birds (24.4% difference).

2. The feeding of the same mash mixed with two parts of skim milk to one part of mash to capons *in pens* (40.4% difference).

3. The feeding of a wet mash composed of equal parts of the same mash and chopped raw potatoes mixed with one part of milk to one part of mash (6.1% difference).

C. Barred Rock Cockerels

1. *Experimental*

For this series of tests Barred Plymouth Rock cockerels were used. The birds were upwards of six months of age on the average, and consequently with a few exceptions were of mature or close to mature body weight. One hundred and forty of the most vigorous and healthy individuals were used for this work and were allotted to the cages of a laying battery according to the method of restricted randomization referred to previously. The detailed technique of feeding and management of these birds has been set forth under the heading of Technique. In this instance one difference in feeding technique was introduced, namely, rather than feeding all wet mashes at a constant ratio of two parts of milk to one part of mash the same quantity of milk was added to each ration, sufficient water being added to give all rations the same consistency when mixed. This procedure was made necessary by the greatly different capacities for absorption of fluids of the grains and mixtures used in this instance. Had this not been done the difference in consitency might have seriously altered the consumption of feeds because of some rations being so dry as to be unpalatable and others so fluid as to cause the birds to very greatly limit their consumption on a dry matter basis. The ratio of actual skim milk to mash was 0.9 : 1 for all pens.

The feeds or treatments given were as follows:)—

Group A.—Ground yellow corn mixed with skim milk.

Group B.—Control—two parts of ground oats to one part of ground barley mixed with skim milk.

Group C.—Cooked potatoes—one part of ground oats, ground barley mash as for pen B to one part of mashed potatoes mixed with skim milk.

Group D.—Ground wheat mixed with skim milk.

Group E.—Meat meal—ground oats, ground barley mixture as for pen B, plus 10% of meat meal, mixed with skim milk.

In addition to the feeds above set forth one-half of each group was allowed only fifteen minutes to consume their feed while the other half was allowed one-half hour.

Where ground grains are indicated the whole grain finely ground was used. In the case of the cooked potatoes as little water as possible was added during cooking and they were steam cooked in a double boiler. Hence all added water was evaporated and nothing was drained off from the potatoes and discarded.

2. *Results*

Table 2 indicates the results obtained.

TABLE 2.—ACTUAL WEIGHT GAIN, ADJUSTED WEIGHT GAIN AND CONSUMPTION OF DRY MATTER FOR ALL GROUPS

Group	Actual gain	Adjusted gain	Consumption Dry matter
	gms.	gms.	gms.
A.—Corn	311.4 ± 45.3	378.8 ± 16.79	2408.0 ± 87.7
B.—Control—2 oats : 1 barley	266.6 ± 30.8	246.8 ± 16.18	2535.2 ± 91.7
C.—Cooked potatoes	248.3 ± 23.41	196.3 ± 16.79	2575.0 ± 68.5
D.—Wheat	321.1 ± 23.6	319.0 ± 16.47	2638.9 ± 72.9
E.—2 oats : 1 barley + 10% meat meal	289.4 ± 31.4	296.7 ± 16.18	2521.9 ± 77.1
15 minutes feeding	281.1 ± 18.4	293.1 ± 10.12	2484.4 ± 37.7
30 minutes feeding	293.2 ± 21.1	282.4 ± 10.23	2584.5 ± 51.2

3. *Discussion*

In considering actual gain it may be noted that the group receiving cooked potatoes gained considerably less than the groups fed whole corn and whole wheat which were outstanding. All other differences were sufficiently small to be of little if any significance. A notable feature of the data is the small dry matter intake by the birds of the corn fed group in comparison to other groups and the large amount of gain which these birds made.

Since as previously indicated the adjusted gain gives a comparison upon a sounder basis these figures should be considered. It is immediately apparent that ground yellow corn is outstanding. The difference in favour of the corn pen over the control pen is 42% and is highly significant. This pen also exceeds the cooked potatoes, wheat and meat meal groups

by amounts of 63.5%, 17.1% and 24.1% all of which differences are highly significant. In this connection it should be pointed out that yellow corn produces yellow fat and is therefore objectionable where white fleshed birds are required as on the Canadian and particularly Old Country markets. Information is not available as to whether white corn would be equally efficient in fattening poultry. However, Braman *et al.* (2) using the paired feeding method with rats and using body and excreta analyses as criteria studied the comparative value of yellow and white corn. The yellow corn ration produced a favourable effect on appetite and a superior gain in weight (protein and water), while the white corn ration excelled in digestibility of food energy and in supporting body gain of energy (fat). The vitamin A deficiency of the white corn ration was not compensated for in these experiments; consequently, both palatability and weight gain might have been increased on the white corn ration had this been done. It would appear to be highly probable therefore, that white corn would be at least as efficient as yellow corn in fattening poultry. It will also be noted that both the wheat and meat meal groups were definitely superior to the cooked potato group by amounts of 47.6% and 40% respectively. The differences between the wheat, and meat meal pens were small and of no significance. In the case of the addition of 10% of meat meal to the fattening mash a significant difference was also found to exist (18%) in favour of the meat meal. Wheat also was found to be more efficient than the control ration, the difference being significant and of the order of 25%.

Between the two feeding treatments, namely a 15-minute feeding period as against a 30-minute period, there is apparently nothing to choose, the difference in weight gains being only 3.7% and not significant.

4. *Summary*

The data presented indicate the following:—

1. While corn and wheat gave similar increases in weight (actual gain) in fattening, judged upon the basis of the efficiency with which these grains were used (adjusted gains) corn was decidedly superior (difference 17.1%) to wheat as well as to all other feeds used in this test.

2. The use of a wet mash of two parts of ground oats to one part of ground barley mixed with skim milk gave less satisfactory results than those obtained with the same ration supplemented with 10% of meat meal (Difference 18%).

3. A mixture of equal parts of the above mash (2 oats : 1 barley) and cooked potatoes, the whole mixed with skim milk, gave inferior results (Difference 22.8%).

4. A feeding period during fattening of fifteen minutes duration was equally as efficient as one of thirty minutes (Difference 3.7%).

II. CRITERIA FOR JUDGING THE ABILITY OF A FEED TO FATTEN

Fattening for market presupposes a change brought about by the addition of fat to the body. For this reason, in crate fattening, feeds which are high in fat and carbohydrates are mainly used. It must be taken for granted, however, that birds which are not entirely mature will continue to grow under fattening treatment, and it is in fact definitely known that increase in weight even in mature birds will not of necessity indicate fat

increase only but that an increase in soluble nitrogenous compounds also takes place (Armsby 1). From the standpoint of the producer, if a bird gains one pound during fattening it means payment to him on the basis of an extra pound, and the nature of the gain is often of little concern. A gain of one pound of fat or mostly fat, however, gives the bird a finish which demands a premium in price for each pound of bird weight and actually puts the bird into the tenderloin class in point of value. Hence the importance of the nature of weight gain in fattening, and an analysis of this gain is in order.

A. Gain in Weight Produced and Percentage of Fat in Tissues

The nature of gain in weight in fattening of growing hogs has been considered by Dunlop (3). He presumed that differences in body weight gain might be due to a different rate of basal metabolism, a different level of efficiency in digestion, or the nature of the weight gained whether protein or fat. He was able to show that the only factor of any real importance was that of the ratio of protein to fat in the body weight gained during growth. That is, one animal might lay down more fat than another but might actually make a much smaller weight gain because the other animal laid down proportionably more protein, a heavier material than is fat (protein being stored with three or more parts of water and fat in almost the pure state.)

In connection with experiments here reported the percentage of fat in various tissues of fattened mature Barred Rock cockerels was determined. It was considered that the percentage of fat in tissue should be correlated with weight gain if the gain actually made was mostly fatty in nature. A correlation between percentage weight gain and percentage of fat in the abdomen was made from data set forth in detail in Table 3. The correlation obtained was $r = +0.065 \pm 0.138$, which is so small as to suggest that no correlation exists between the two factors under consideration in these data. Since from the same data a correlation of $r = +0.82 \pm 0.005$ exists between skin and subcutaneous fat, and abdominal fat, it follows that the body weight gain of any individual is not necessarily an indication of the degree of fatness of that individual as judged by the fat content of abdomen, and of skin and subcutaneous tissues.

The explanation of this rather surprising result appears to be fairly evident, however. It may be presumed that the principle enunciated by Dunlop (3) above referred to would be active in this instance to some extent at least, and that many animals which gained greatly laid down little fat but did lay down protein material or moisture, and others gained little because they laid down much fat which represents much lighter gain than that of protein. If these birds, though for the most part past actual growth (*i.e.*, the development of all tissues: bone, muscle, nervous tissue etc. from a common growth impluse) did, during this period, lay down muscle tissue or increase the moisture content of their tissues, to the extent that this principle operated, the greater the gain made the smaller might be the fat increase and hence a very low correlation would result. In addition it was not possible to measure the increase in fatness during the

test as no measure of degree of fatness was available at the beginning of the experiment. Consequently, the degree of fatness at the conclusion of the experiment would depend to a large extent upon the degree of fatness at its beginning which factor would vary greatly from bird to bird. Consequently one bird which gained well might have a low percentage of fat at the conclusion of the experiment due not to lack of increase in fat, but to the fact that it was quite thin at the commencement of the test. The two factors mentioned then if operative, would both have a tendency to work against amount of weight gain being an expression of the actual degree of fatness of the dressed birds and hence to decrease correlation. On this assumption it would appear, therefore, that weight gain may be a poor indicator of the degree of fatness of a bird and probably also of the actual fat gained during fattening. Until some more efficient technique is devised so that actual increase in fat during any definite period may be measured, it will not be possible to determine accurately the fattening ability of any feed or feed mixture for poultry.

In this connection the methods of obtaining the increase in fat during fattening should be briefly mentioned. In hogs, the average thickness of back fat (4 measurements) was found to be a reliable index of the percentage fat of the carcass with a correlation of 0.84 ± 0.04, by Hankins and Ellis (7). While this measurement in hogs offers possibilities of determining the percentage of fat in the same animal before and after fattening we have been unable as yet to find a comparable measure for poultry of any value for this purpose. It should also be pointed out that to kill and analyse a sample of birds from each group under test before the start of the test as an indication of the degree of fatness of the whole group is of no practical value for this purpose since the variability in fat content between individual birds on the same treatment is so great that an impracticably large sample would have to be taken.

B. Distribution of Fat as Affected by Feeds

Research work in fattening of poultry has recently been published by Maw (9) indicating that not only do different feeds lay down fat at a different rate but that they also cause deposition of fat in different areas. Using corn, barley, oats and wheat, fed simply as the cereal portion of a fattening ration to which 6% of an animal feed mixture of three parts by weight of beef meal to two parts of powdered milk, was added, he found that the corn-fattened birds at the end of the trial had 5.8%, 29% and 69% of fat in the flesh, skin, and abdominal tissue respectively, whereas, the wheat fattened birds contained 3.4%, 34% and 77% respectively. The importance of this finding is obvious when it is considered that from the standpoint of quality a high percentage of fat in the flesh and skin is desirable as is also a low percentage in the abdomen. Presumably a high fat content of flesh and skin would mean a better quality of breast meat, better retention of fat and moisture in cooking, and a superior bloom and finish to the carcass, whereas abdominal fat is largely wasted or used only for frying or shortening.

Thus, in order that the comparative fattening efficiency of two feeds be determined it would be necessary not only to determine the ability of

the feeds to lay down fat but also to lay down fat to a greater extent in the more desirable locations in the carcass, namely, breast and skin. As a result of this work the fattening tests here reported upon were designed to determine distribution as well as quantity of fat. At the end of three weeks of fattening, the carcasses of twenty-one dressed roasters from each of two pens on different feeds were analysed for percentage of fat in breast muscle, in skin and subcutaneous tissue, and in abdominal tissue, details of the technique of such analyses having been given in an earlier section of this publication. The detailed results of these analyses are given in Table 3.

In considering the data in Table 3 it will be noted particularly that any differences which occur in the mean percentage of fat of the two groups for comparable tissues are extremely small and are in no way significant. It is apparent therefore, that the birds fed on the two grains were in approximately the same degree of fatness at the end of the test. Not only is this the case, but the ratios of fat in breast to fat in skin and subcutaneous tissues and to fat in abdomen for both groups are remarkably constant, *viz.*, 1 : 32.7 : 48.0 for corn, and 1 : 33.8 : 50.6 for wheat. In order to analyse more critically the relationship between the percentage fat in the different tissues a covariance analysis of the data was made, the results obtained being set forth in Table 4.

With regard to variance as indicated in this table, since the variance within the groups of each treatment is either equal to or much greater than that between treatments for breast fat, skin and subcutaneous fat, and abdominal fat, there is therefore no significant difference in degree of fatness whether corn or wheat was fed. In so far as the distribution of fat is concerned the correlations are particularly informative. A high and significant correlation exists between the percentage of skin and subcutaneous fat and that of abdominal fat. In other words, as the fat level of the skin and subcutaneous tissues increases so also does the fat level of the abdominal tissue, and almost in like proportion as shown by the regression of skin and subcutaneous fat upon abdominal fat shown in the table indicating that for every increase of 1 unit in skin and subcutaneous fat there was an increase of 1.1 units in abdominal fat. Between percentage of breast fat and the other two measures the correlations are either not significant or barely significant, and sufficiently low as to be of no practical importance. Since apparently breast fat and these other measures are not correlated to any appreciable degree it is interesting to note that when the effect of breast fat is removed from the calculation the correlation between skin and subcutaneous fat, and abdominal fat becomes $r = +0.93 \pm .0007$, a practically perfect correlation. The magnitude of the correlations between treatments, while they indicate that such a correlation does exist, is of no importance with only one degree of freedom. The fact that the taking out of the variance and covariance between treatments did not alter the residual correlation of within treatments from that of the total indicates that both the corn and wheat fattened birds belong to the same population and do not differ significantly in their relationships including the areas in which their fat is distributed.

In order to further substantiate this finding it was planned to analyse twenty-one birds from the pen which had received a mash mixture of

TABLE 3.—PERCENTAGE FAT IN BREAST MUSCLE, SKIN AND SUBCUTANEOUS FAT AND IN ABDOMINAL FAT FOR CORN AND WHEAT FATTENED BIRDS

A.—Corn					D.—Wheat				
Bird No.	Breast %	Skin and sub. %	Abdominal %	Gain %	Bird No.	Breast %	Skin and sub. %	Abdominal %	Gain %
70	1.34	45.5	65.3	23.8	53	1.11	43.2	68.9	9.2
92	1.05	57.2	83.7	8.5	83	1.57	41.4	65.0	10.8
30	1.62	41.4	56.2	18.3	32	1.11	38.1	60.8	10.0
79	1.24	36.0	61.7	15.3	28	1.66	43.6	61.8	8.2
113	1.32	44.0	69.5	7.0	13	1.30	50.4	72.4	12.8
135	1.52	39.9	66.6	14.9	8	0.93	46.2	69.9	7.4
122	1.36	51.5	69.4	16.0	104	0.89	40.8	65.9	8.8
84	0.66	33.3	47.6	6.9	24	1.09	38.9	64.1	5.5
21	1.62	45.2	63.6	6.4	73	1.64	50.3	73.7	11.2
138	1.58	49.2	62.6	13.7	112	1.62	51.3	77.5	6.5
58	1.33	43.4	60.9	8.7	66	1.23	42.5	53.0	8.7
6	1.13	33.7	49.4	−2.9	76	1.02	35.2	46.6	5.5
43	1.26	54.5	69.8	18.4	116	0.97	30.4	49.4	10.3
3	2.20	40.1	53.9	10.2	109	1.29	45.5	71.6	7.1
15	0.97	32.2	52.9	6.8	341	1.45	37.8	58.4	14.9
51	1.26	42.7	68.9	10.7	88	1.37	43.7	62.0	16.8
20	1.40	59.1	79.4	7.1	121	1.33	47.9	68.5	11.1
103	1.51	43.6	64.6	11.5	97	1.65	50.3	65.8	17.5
47	1 56	53 6	78.3	10.5	39	0.92	40.4	68.6	14.2
129	1.14	41.9	74.0	11.3	64	1.24	37.8	52.6	8.0
99	1.59	46.7	62.7	20.0	94	1.36	47.4	73.5	13.8
N	21	21	21	21	N	21	21	21	21
Total	28.66	934.7	1361.0	246.0		26.75	903.1	1350.0	218.4
Mean	1 36±0.069	44 5±1 70	64.8±2.02	11.71±1.26		1.27±0.057	43.00±1.25	64.29±1.86	10.40±0.76

TABLE 4.—VARIANCE, COVARIANCE, CORRELATIONS AND REGRESSIONS FOR PERCENTAGE OF FAT IN BREAST, PERCENTAGE OF FAT IN SKIN AND SUBCUTANEOUS TISSUE AND PERCENTAGE OF FAT IN ABDOMINAL TISSUE FOR CORN AND WHEAT FED BIRDS

		Percentage of breast fat (a)		Percentage of skin and subcutaneous (b)		Percentage of Abdominal fat (c)		Sums of products			Correlations			Regressions		
Source of variance	D/F	Sum of squares	Mean square	Sum of squares	Mean square	Sum of squares	Mean square	ab	ac	bc	ab	ac	bc	ab	ac	bc
Total	41	3.31	0.081	1806.4	44.1	3250.2	79.3	28.5	16.7	1989.3	0.37 *(0.304)	0.16	0.82	8.61	5.05	1.10
Between treatments	1	0.089	0.089	23.7	23.7	2.88	2.88	1.42	0.48	8.28	0.98 *(0.997)	0.95	0.99			
Within treatments	40	3.23	0.081	1782.7	44.5	3247.1	81.2	27.1	16.3	1981.0	0.36 *(0.304)	0.16	0.82			

* Level required for significance (P = 0.05).

two parts of ground oats to one part of ground barley with skim milk. After seven birds had been analysed however, the results with regard to distribution of fat were sufficiently similar to those from the corn and wheat fed groups that it was felt that the labour of sampling and analysis of the remaining fourteen birds would have been superfluous. The mean percentage of fat found in the various tissues of these birds is shown herewith, together with the same figures for the wheat fed birds for purposes of comparison.

	Percentage of fat	
	Oats + barley	Wheat
Breast	1.26 ± 0.150	1.27 ± 0.057
Skin and subcutaneous	43.15 ± 3.10	43.00 ± 1.25
Abdominal	65.92 ± 3.52	64.29 ± 1.86

A covariance analysis indicated a significant correlation of 0.747 between percentage fat in skin and subcutaneous tissue and that in abdomen thus substantiating for this feed mixture as well that fat is distributed in a definite and similar ratio in the depot areas, regardless of the feed given.

These results appear to throw some light upon the manner in which fat is deposited. It appears obvious that skin fat, subcutaneous fat, and abdominal fat represent depot fats which are laid down simultaneously. It would seem that the fat in the blood stream must be deposited in the adipose tissue either in relation to the amount of that tissue or to blood supply of that section of the body. Consequently while a greater supply is laid down in the abdomen, a definite proportion between such fat and that of other depot areas such as the skin and the subcutaneous fat exists. Consequently it would seem reasonable to suppose that no matter what the nature of the fat in the blood stream (whether from wheat or corn for example) the rate of deposition in any area is governed by physiological factors which are not likely to be affected by extraneous factors such as the nature of the fat itself. Since the differences which exist in the fat of wheat and corn are very slight it might well be that such small differences are not sufficient to upset the physiological routine of the blood stream.

The fact that percentage fat in breast muscle is correlated only slightly with percentage skin and subcutaneous fat and not at all with percentage abdominal fat is worthy of comment. In considering the data presented in Table 3 it will be seen that the mean level of fat in breast muscle was 1.32% (both pens combined). This figure in itself is so low in comparison to 43.7% for skin and subcutaneous and 64.5% for abdominal fats as to suggest that breast muscle is not the recipient of depot fat to any great degree and that the 1.32% found probably consists largely of the more complex fats as cholesterol and lecithin which are a part of the functioning cell and not of a depot nature. That this may well be the case is further strengthened by work of Terroine (11) which indicated that these fats persist in the tissues of birds dead of starvation and from which the depot fats have been completely exhausted. In two species of Weaver birds although normally 8.7% of fat was present in the entire body with great variability from bird to bird, after starvation to the point of death a very constant level of 2.16% was found with a variability of only 7.8%. Making allowance for the fact that other tissues (thigh for example) when free from

adhering depot or interstitial fat have a slightly higher level of fat than that of breast tissue, and for probable species differences, the figure of 2.16% is quite comparable to the 1.32% of these data. It seems probable therefore, that fat is deposited in breast tissue only in minute quantities except as a component part of the cell and therefore at a relatively fixed level for any one bird; consequently the nature of the feed given would be expected to have little, if any, effect upon the percentage of fat in the breast. It should be noted that in even the fattest of these birds breast fat was not above 2.2%, and this individual showed a much higher value than most of its pen mates.

C. Apparent Finish

In so far as the marketing of dressed poultry is concerned apparent finish, which in reality means fine texture of skin, presence of fat in the skin and subcutaneously, and probably other less tangible factors summed up in the trade by the term "bloom," is one of the most important factors in the presentation of a carcass of pleasing appearance which is readily saleable. Without doubt the percentage of fat in the skin and subcutaneously (which is visible through the skin) contributes materially to finish. Consequently, the importance of giving market birds feeds which not only produce large weight gains but gains which are mostly made up of additions of fat to the tissue becomes apparent and emphasizes the importance of judging the value of fattening feeds by the increase in fat which they bring about rather then weight gains. Since it seems to be the case that different feeds probably have no effect upon the location in which fat is distributed, improvement in finish must come about either by increasing the gross amount of fat in the bird, in which case the more or less waste fat of the abdomen must be accepted as a necessary evil, or by changing the nature of the fat deposited according to the degree of saturation of the fats given, a matter which is fairly readily accomplished in poultry as indicated by the work of Halnan and Cruickshank (6) and Cruickshank (4), although this is not necessarily the case with some other animals as shown by Thomas *et al.* (12).

D. Summary

The data here presented show that gain in weight during fattening, while an exact measure of the actual gain in tissue, may be a very poor criterion of the degree of increase of fat or of the degree of fatness of the bird. One of the reasons for this without doubt is the fact that since different birds at the start of a fattening period will possess different levels of body fat, the percentage fat of the dressed bird will give little indication of the actual increase in fat; consequently, this measure of fatness, which represents the only practical technique of determining increase in fat at the present time is not good a indication of the actual weight increase or vice versa.

The data presented also indicate that the level of fat in the skin and subcutaneous tissues and in the abdomen are very closely correlated, and it may be considered therefore that fat is deposited in these areas at a very definite rate thus showing a constant ratio between the two. It was also found that little fat is added to breast muscle during fattening and that

this tissue does not appear to be a part of the body where depot fat is laid down. These relationships existed to the same degree regardless of the different feeds given in this experiment; consequently it may be concluded that the nature of the fattening food given, in this case at least, while it may affect the amount of fat deposited does not in any way change its distribution in different parts of the body.

GENERAL DISCUSSION

Since very little controlled experimental work has been carried out in recent years in the fattening of market poultry the technique of such trials is not well established. As a consequence the experiments reported herein have been concerned largely with technique as well as actual fattening results from different feeds and treatments. In the matter of experimental procedure, the most satisfactory criteria of efficiency of a feed or treatment for fattening purposes have been investigated. In the past, with few exceptions, the criterion used to measure this efficiency has been gain in weight produced or the amount of feed required to produce a definite unit of gain sometimes known as the gain-feed ratio. Since the process under consideration is one of fattening, the weight gain is of importance chiefly to the extent to which it is a reflection of actual gain in fat. Hence, the increase of fat during a fattening test is the factor of greatest importance in the success or failure of a fattening operation. In order to determine, however, what proportion of this fat represents an increase due to a definite feed or treatment, the level of fat prior to fattening as well as at the end of a fattening period is essential.

In addition to the criteria of efficiency in fattening, the actual technique of fattening trials has been investigated. The uncontrolled variables of greatest importance in a fattening test are the varying initial weights of the birds and the variable rate of feed consumption. The former has been controlled in these experiments by two methods, namely, that of random allotment between pens upon a restricted basis, the restriction being initial weight, and by the adjustment of the weight gains by the regression of initial weight upon weight gain. In adjusting the means for the regression of initial weight upon weight gain in a population in which initial weight had already been equalized as far as could be done by restricted random allotment, it was found that very little adjustment from the actual means was necessary; hence the two methods were apparently similar in efficiency. In view of the nature of the two methods however, the method of adjustment by regression is probably the most desirable and is less laborious in actual process. The variable rate of feed consumption was also adjusted by two methods. The first was by actual restriction of feed intake on the basis of the surface area of the bird. It was found impossible to adequately restrict feed consumption in this manner, however, and the second method, the adjustment of the mean weight gains by the regression of feed consumption on weight gains, was used with entire satisfaction. By adjusting weight gains by the partial regressions of initial weight and feed consumption upon these gains, a reduction in the variability due to these uncontrolled factors was brought about sufficient to reduce the standard deviation from 166.9 to 85.6, thus very greatly increasing the sensitivity

of the test. Since this method of adjustment has been set forth elsewhere (Gutteridge 5), detail of the procedure is not given herein.

A technique of sampling of dressed experimental birds for determination of percentage of fat in tissues was devised in such a manner as to give a representative picture of the fat content of the bird as well as of the portions of the bird in which the level of fat is of the greatest practical importance. A macro-method of fat determination for these samples is also set forth in detail.

In view of a suggestion met with in the literature that different feeds significantly alter the region of deposition of fats in the body this matter was investigated. Such a possibility could not be confirmed by these data.

In addition to the technique of fattening trials two series of actual fattening tests are reported in detail herein, one in which White Leghorn capons were used as subjects and the other with Barred Rock cockerels.

SUMMARY

A. Fattening Trials

On the basis of weight gain at the same initial body weight and at the same level of feed consumption the following conclusions may be drawn.

1. The feeding to crated birds of a fattening mash in the dry state with skim milk to drink, both being before the birds at all times, gave definitely inferior weight gains to the feeding of the same mash moistened by twice its weight of skim milk and fed twice daily for feeding periods of one-half hour.

2. Pen feeding of White Leghorn capons as opposed to feeding in fattening crates was relatively inefficient.

3. The feeding of a fattening mixture of equal parts of mash and potatoes, whether raw or cooked, mixed with skim milk, gave definitely inferior results to the feeding of the same mash not thus supplemented.

4. Ground yellow corn when mixed with skim milk was decidedly more efficient than ground wheat plus skim milk or a mixture of two parts of ground oats to one of barley plus skim milk.

5. A mash mixture of two parts of ground oats to one part of ground barley to which meat meal at a level of 10% of the mash mixture was added was superior to the same mash mixture not thus supplemented.

6. A feeding period of fifteen minutes during fattening was as efficient as one of thirty minutes.

B. Technique

1. Weight gains in dressed poultry are not a satisfactory indication of the efficiency of a feed or treatment to increase fat in fattening birds.

2. Owing to the great variation which naturally will occur in the degree of fatness of different birds at the beginning of a fattening test the percentage of fat in tissues at the end of the test may be a poor criterion of the increase in fat during the experiment.

3. The technique of sampling of individual dressed birds from fattening experiments by which representative samples of the tissues of most importance from the standpoint of quality of dressed poultry may be taken as well as the method of chemical analysis for such samples set forth herein were found to be highly satisfactory for the purpose.

4. The most important uncontrolled variables in fattening experiments, namely, variation in initial weight and in feed consumption, have been investigated and the actual weight gains adjusted for the effect of these variables by two methods in each case. The method of adjustment of weight gains by the partial regressions of the uncontrolled correlated variables upon those gains was shown to greatly increase the efficiency of fattening experiments.

5. Different cereals (in this instance corn, wheat and a mixture of oats and barley) had no effect upon the amount of fat laid down in different parts of the body. Consequently the distribution of fat as a criterion of the fattening efficiency of a feed may be neglected under similar circumstances to those pertaining in this test.

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Résumé

L'engraissement des volailles—Méthodes et rations. H. S. Gutteridge, aviculteur, Ferme expérimentale centrale, Ottawa.

En se basant sur l'augmentation de poids réalisée à partir d'un même poids initial du corps et lorsque la quantité de nourriture employée est la même, on peut tirer les conclusions suivantes:—Les oiseaux tenus en épinette qui recevaient une pâtée sèche, accompagnée de lait écrémé comme breuvage, ces deux aliments tenus devant eux en tout temps, ont fait une augmentation de poids bien inférieure à celle qui a été enregistrée par les oiseaux recevant une pâtée humectée par deux fois son poids de lait écrémé et distribuée deux fois par jour pendant des périodes d'alimentation d'une demi-heure. L'engraissement en parquets de chapons de la race Leghorn blanche ne peut être comparé, au point de vue de l'efficacité, à l'engraissement en épinettes. D'autre part, l'emploi pour l'engraissement d'un mélange en parties égales de pâtée et de pommes de terre, crues ou cuites, mélangé avec du lait écrémé, a donné des résultats bien inférieurs à ceux donnés par la même pâtée dépourvue de pommes de terre. Le maïs jaune moulu mélangé avec du lait écrémé s'est montré beaucoup plus engraissant que le blé moulu additionné de lait écrémé ou qu'un mélange de deux parties d'avoine moulue et d'une partie d'orge additionné de lait écrémé. Un mélange de pâtée composé de deux parties d'avoine moulue et d'une partie d'orge moulue, auquel on ajoutait de la poudre de viande à raison de 10% de la pâtée, s'est montré supérieur à la même pâtée dépourvue de poudre de viande. Une période d'alimentation d'une durée de quinze minutes pendant l'engraissement a été trouvée aussi efficace qu'une durée de trente minutes. L'augmentation de poids constatée chez les volailles habillées n'est pas une indication satisfaisante de l'utilité des aliments ou du traitement pour augmenter la couche de graisse chez les oiseaux. Etant données les variations considérables qui se produisent naturellement dans le degré d'engraissement des oiseaux au commencement des périodes d'engraissement, le pourcentage de graisse dans les tissus à la fin de l'essai peut être une pauvre indication de l'augmentation de graisse qui se produit pendant l'expérience. La technique qui consiste à prélever des échantillons de différents oiseaux habillés soumis à des essais d'engraissement et qui permet prendre des échantillons représentatifs des tissus les plus importants au point de vue de la qualité des volailles, de même que la méthode d'analyse chimique de ces échantillons exposée dans cet article a été très satisfaisante pour cela. Les plus importants des facteurs qui échappent au contrôle dans le système d'engraissement, savoir la variation dans le poids initial et dans la consommation de la nourriture, ont été étudiés et les augmentations réelles de poids ont été ajustées au moyen de deux méthodes dans chaque cas pour trouver l'effet de ces facteurs. On a constaté que la méthode qui consiste à ajuster l'augmentation de poids par la régression partielle sur cette augmentation des facteurs variables, reliés et non contrôlés, augmente beaucoup l'utilité des essais d'engraissement. Les différentes céréales (dans le cas qui nous occupe le maïs, le blé et un mélange d'avoine et d'orge) n'ont eu aucune influence sur la quantité de graisse déposée dans les différentes parties du corps. Dans les circonstances semblables à celles dans lesquelles cet essai a été conduit, on peut donc ne pas tenir compte de la distribution de la graisse comme indication de l'effet engraissant des aliments.

FECUNDITY AND REPRODUCTIVE ABILITY IN CLOSELY CONFINED FOWL[1]

S. Bird[2]

Central Experimental Farm, Ottawa, Canada.

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It has frequently been observed that fecundity may suffer severely in closely confined fowls and that their reproductive ability may be interfered with under such environment. In the following notes various observations, bearing on these problems, will be briefly summarized.

MATERIAL

Through the three years, from the fall of 1932 to the fall of 1935, experiments have been conducted at this Division in which all birds were individually caged. The environment, feeding and other factors in handling were so essentially alike for all groups that no attempt at differentiation between the groups has been made on these counts. The rations were made up of 50% mash and 50% scratch grain, this latter being ground finely and incorporated in the mash. The mash consisted of the ordinary mixture of cereals and milling by-products with admixtures of 13% animal protein from a good grade of fish meal, meat and bone meal, bone meal and skim milk powder; ½% NaCl and 1% cod liver oil were added to the total rations. In addition the birds had access to crushed oyster shell *ad lib* and tap water to drink.

In all groups weekly determinations were obtained for each bird, of its body weight, the weight of eggs laid, and the separate quantities of food and of oyster shell ingested.

For controls comparable birds of similar breeding kept under normal pen environment have been used, and, in addition, free use has been made of records culled from the literature.

Throughout the following analyses, the records of surviving birds only have been used.

ANALYSIS OF RESULTS

Fecundity

Mean egg production from four groups of caged birds and from two control groups from normal pen environment are recorded in Table 1.

TABLE 1.—FECUNDITY IN FOUR LOTS OF INDIVIDUALLY CAGED BIRDS, AND IN TWO CONTROL LOTS

Group	Year	Environment	No. birds	Breed	No. days in laying year	Mean no. eggs	C.V.	Per cent production
A	1932–33	Cage	37	B.R.	308	178.5	12.4	58.0
B	1932–33	Cage	36	W.L.	308	146.1	26.5	47.4
C	1933–34	Cage	116	B.R.×W.L.	280	173.0	14.8	61.8
D	1933–34	Pen	52	B.R.×W.L.	336	182.6	26.9	54.3
E	1934–35	Cage	95	B.R.	285	168.3	19.3	59.0
F	1934–35	Pen	97	B.R.	308	192.2	20.3	62.4

[1] Contribution from the Division of Poultry Husbandry.

[2] ————————.

It will be noticed that under the caged environment, variability as expressed by the coefficient of variability has been reduced to about 75% of that obtained under pen conditions for comparable rates of production. It is also noticeable that there is an inverse relationship between rate of production and magnitude of variability.

The variabilities found in groups D and F are presumably typical of normal conditions, Dudley (18), Munro (33), and it is therefore evident that the caged environment in some way is a favourable one.

In Figure 1 is presented the frequency polygons of egg laying for Group C and its direct control Group D. In Figure 2, likewise, is presented the polygons for Group E, its control Group F and for Group A which was made up of very closely comparable birds. In the graphs, production in all groups has been adjusted to a comparable basis by calculating simple pro rata values for 308 days, and for 116 and 94 birds in Figures 1 and 2 respectively. It will be seen from these graphs that the distributions for the caged groups are in all cases quite close to symmetrical and with high degrees of curtosis. The smaller variability in these groups is secured by elimination of the extreme parts of both the high and the low "tails" and in many instances by the smaller number of observations in these and adjoining classes. It is therefore evident that caging is beneficial to the extent that this environment will permit a good proportion of the poorest and fairly poor birds to make better records. At the same time there is undoubtedly an inhibiting factor which prevents the best birds from making as good records as the better birds may do under pen conditions, see especially Figure 2. From the mean values presented in Table 1 it will be seen also that the detrimental factor very frequently may be the stronger

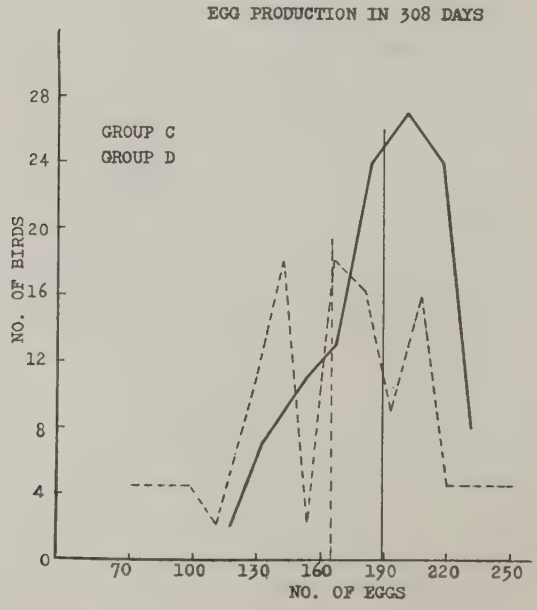

FIGURE 1

of the two, probably affecting the greater number of all the birds in a group, thereby shifting the entire distribution towards the low values with a consequent lowering of the mean.

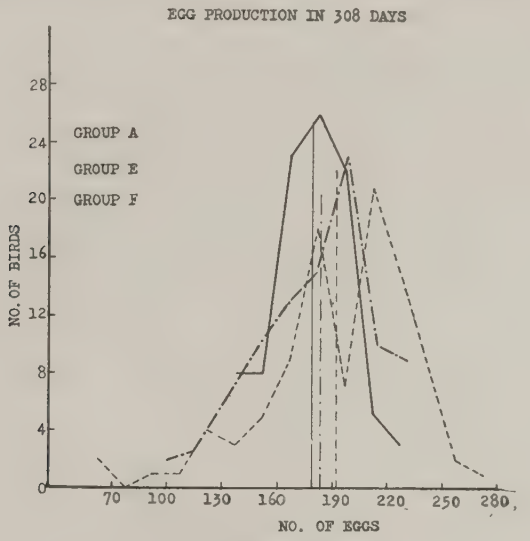

FIGURE 2

Reproduction

Our evidence concerning reproduction is seemingly quite contradictory.

The birds of Group A were individually mated to healthy vigorous males which also had been kept in cages. On microscopical analysis the sperm of these males was found to be essentially normal. Approximately 500 eggs were set from these matings showing a mean fertility of 27.5% with a hatchability from fertile eggs of 22.7%.

During the same season nearly 700 eggs were set from 63 birds of essentially the same breeding that had been under normal pen environment. The mean fertility of these settings proved to be 82.5% and mean hatchability from fertile eggs was 54.4%.

A covariance, correlating rate of production to hatchability in these last mentioned settings, was calculated. In this study the number of eggs set from each bird per week was assumed to be indicative of the individual rates of production.

TABLE 2.—COVARIANCE FOR RATE OF PRODUCTION TO PER CENT HATCHABILITY

——	D.F.	X Per cent production		Y Per cent hatchability		Covariance		
		Σ sq.	Mean sq.	Σ sq.	Mean sq.	Σ prod.	r	b_{yx}
Between males	9	949.0	105.4	11897.2	1321.9	483.6		
Within males	53	18252.2	344.4	24125.7	455.2	11076.6	0.528	0.609
Total	62	19201.2		36022.9		11560.2		

This calculation shows an appreciable and highly significant correlation between the two factors, and a regression of 6.1% increase in hatchability for every 10% increase in fecundity. This is probably very true to the normal occurrence and is supported by the evidence brought forward by Jull (26), Byerly, Titus and Ellis (11) and Russel and Tayler (38). Until the time when the eggs were set the birds of Group A had a mean rate of intensity of 73.8%. It is therefore evident that fertility and hatchability results from this group were quite subnormal.

In contrast to the hatchability results obtained from the caged Group A, above, are the observations obtained three years later in Group E which was also caged. During the last three days of May, 1935, 30 females of Group E and 14 of Group F were artificially inseminated. The sperm was secured from the vas deferens of 12 young males and was possessed of maximum degree of motility in every case according to Munro (32). Each bird was inseminated only once and all eggs laid for the following fourteen days are accounted for in this analysis. Two hundred and fourteen eggs were set from Group E and 115 from Group F. The mean rates of production were 51 per cent and 55 per cent, respectively. Results of a variance analysis of fertilizing and hatching results are presented in Table 3.

It will be appreciated that there does not appear to be any significant difference between results obtained under the two contrasted environments either with regard to fertility or to hatchability and that this test, therefore, seemingly constituted a direct contradiction to our previous experience. Moreover, the mean hatchability for these caged birds is of the same order as that previously described for entirely normal conditions, namely 54.4%. However, the difference between mean hatchabilities in Table 3 amounts to $\left(73.1 - 59.5/\frac{73.1 + 59.5}{2}\right) \times 100 = 20.5\%$, and the inability to demonstrate significance on such a difference is due to the high mean coefficient of variability which amounts to 44.1%. According to Bird and Gutteridge (4) it would require observations on twice as many birds as those actually employed in order to demonstrate a significant difference under our experimental conditions. It may therefore be said that although this test failed clearly to demonstrate inferior hatchability from caged birds, there was still a tendency in this direction. The percentage fertility encountered in this test was significantly lower than the 82.5% recorded previously for control conditions. Presumably this is due solely to the fact that in these last tests only one insemination was employed, with eggs being collected for fourteen subsequent days. The average fertility in the caged birds was 76.4% for the first seven days and only 49.9% for the last half of the collection period.

It is evident from these results that approximately normal fertility and hatchability may, under certain conditions, be obtained from caged birds. Our evidence is however insufficient entirely to account for the various aspects of the problem. For instance, did the caged environment in some way tend to alter the physiology of the females? Did the artificial insemination tend to overcome such alterations in the female physiology, or did the fact that the males serving Group A females had been caged, and those employed for insemination of Group E females had been under pen conditions account for the difference in results? The evidence of

TABLE 3.—RESULTS FROM ARTIFICIAL INSEMINATION OF BARRED ROCK FEMALES, 1935

		Fertility							Hatchability of fertile eggs						
		D.F.	Sum of squares	Mean square	F	5%	M.	C.V.	D.F.	Sum of squares	Mean square	F	5%	M.	C.V.
Group F Pen	Between males	3	9177.6	3066.5					2	3440.7	1720.4				
	Within males	10	6807.9	680.8	4.51	3.71	45.5 ± 8.26	57.4	7	4973.5	710.5	2.42	4.74	73.1 ± 10.10	36.4
	Total	13	15985.5	1229.7			45.5 ± 9.39	77.1	9	8414.2	934.9			73.1 ± 9.68	41.8
Group E Cage	Between males	7	15414.4	2202.0					7	24129.0	3447.0				
	Within males	22	21851.2	993.2	2.49	2.46	54.7 ± 6.72	57.6	17	16172.1	951.3	3.62	2.61	59.5 ± 7.49	57.8
	Total	29	37265.6	1285.0			54.7 ± 6.53	65.4	24	40301.1	1679.2			59.5 ± 8.20	68.9

Significance of Differences within Males

$$\frac{54.7 - 45.5}{\sqrt{6.72^2 + 8.26^2}} = 0.86 : P = 0.39$$

$$\frac{73.1 - 59.5}{\sqrt{10.10^2 + 7.49^2}} = 1.08 : P = 0.28$$

Significance of Differences of Totals

$$\frac{54.7 - 45.5}{\sqrt{6.53^2 + 9.39^2}} = 0.80 : P = 0.42$$

$$\frac{73.1 - 59.5}{\sqrt{9.68^2 + 8.20^2}} = 1.07 : P = 0.28$$

TABLE 4.—SHOWING DISTRIBUTION OF FULL-SISTERS

Mated to		Produced	
		Full sisters	
Sire No.	Dam No.	1st year in Cage Group F	1st year in Pen Group E
775	27	1	2
745	31	1	1
774	31	2	1
774	33	2	1
782	46	1	1
780	77	3	1
780	81	1	1
779	81	1	1
778	81	2	1
778	87	1	2
		15	12

microscopical analysis of sperm samples tended to refute this last supposition. There are, however, far too many questions to be answered at once, and for the present the problem must be left as it stands.

After completion of the pullet year, all birds retained from Groups E and F were run together in pens. At mating time, in February of 1936, 15 birds from Group E and 12 from Group F, which together constituted 7 small full-sister groups, were mated to 7 males in the manner shown in Table 4.

In this way ten small full-sister group matings were secured. When the average hatching results were calculated from the records of any two or three birds from the original Groups E and F that occurred in any one mating, it proved possible to obtain 10 paired observations. The hatching results from these pairs were analysed by the appropriate method and gave the results shown in Table 5.

TABLE 5.—SECOND YEAR'S HATCHING RESULTS. NATURAL MATINGS.

First year's environment	Fertility			Hatchability of fertile eggs			Mortality to three weeks		
	Mean %	t	p	Mean %	t	p	Mean %	t	p
Floor	82.76	0.968	0.35	71.56	1.156	0.30	8.10	1.625	0.15
Cage	77.85			64 40			4.65		

The difference in mean fertility is 6.1% and in mean hatchability is 10.5%. The advantage of the floor birds over the caged sisters in the last named character was through the ten pairs −1.8, −27.5, +34.4, +20.0, +33.4, −4.7, −12.3, +21.8, −6.0, +14.3. What small tendency towards a real difference in hatching results there may have been while the difference in environment was in force has, therefore, entirely disappeared when this difference was eliminated for a short period of time.

ANALYSIS OF CAUSES

In the foregoing it has been shown that confinement in cages may impose certain limitations on the fecundity and reproductive ability of domestic fowl. In the following discussion an attempt will be made to investigate some of the causes for these disturbances.

Abnormalities

Certain events recurred with sufficient regularity to mark them as definite subnormalities. In all of these cage groups egg shells became noticeably thin, even to the point where it would be practically impossible to recover any but broken or shell-less eggs from individual birds. Miller and Bearse (31) showed that the quality of egg shell declined gradually throughout the laying year and that high production is coincident with poor shell quality and texture. However, the lack of or decline in deposition of calcium on the membranes of eggs in this experiment was very pronounced and became noticeable as early in the year as March and April, which would clearly indicate a subnormality in these birds. In birds from Groups A and C, and a Group G which will be referred to later, the bones had suffered severe injury from decalcification. In all of our caged birds nervous excitability was quite pronounced. However the most generally occurring characteristic in all of these groups was pauses in egg laying. These pauses appeared from the beginning of March onward. They might last for seven to fourteen days or they might be extended over several weeks or months. In addition these pauses would, on frequent occasions lead directly into moults or broodiness.

Calcium and Phosphorus as the Limiting Factors

The poor egg shells, the decalcified bones and the nervous excitability definitely point to a situation in which calcium has been the deciding limiting factor. Whether such deficiency is mainly in the nature of a faulty calcium to phosphorus ratio, whether the quantity of calcium has been at fault or whether a deficiency in utilization of calcium has been the cause, is not readily apparent. However, it will be shown that for caged birds the quantitative nature of the situation is obvious and that all the other disturbances, in all probability, were but ramifications of this one fundamental limitation.

Phosphorus

The total rations contained by analyses, approximately 0.95% P. In their above mentioned work Miller and Bearse (31) concluded that 0.8% P in the ration was optimum for high egg production on two different levels of calcium. However, it may be seen from their data that egg laying on the 0.8% level of P was not significantly different from that which occurred on 1.04 or 1.08% P, whereas it might be shown by the binomial method of Miles (30) that practically identical levels of phosphorus always gave poorer results on the higher level of calcium. It would therefore be logical to assume that their phosphorus levels of 0.8 to 1.1% were too low on heavy calcium consumption and that therefore our level of 0.95 P, which frequently accompanied the much heavier calcium consumption necessary for optimum production in our birds, may have been inadequate and thus constituted a limiting factor. These findings however do not agree with the work of Common (14). In individual balance studies this author obtained greatly superior results on a $CaO : P_2O_5$ ratio of 3.33 : 1 than he did on a ratio of 0.38 : 1, employing practically the same level of

phosphorus on the two different ratios. Table 6 shows the high and low values employed by Miller and Bearse, Common, and in our rations.

TABLE 6.—RESULTS OF LEVELS IN CaO AND P_2O_5 IN POULTRY RATIONS

	Superior			Inferior		
	CaO	P_2O_5	Ratio	CaO	P_2O_5	Ratio
	%	%		%	%	
Miller and Bearse	2.22	1.95	1.13	3.00	1.81	1.66
Common	3.1	.93	3.33	.365	.979	.037
Ottawa	6.1	2.18	2.80	1.5	2.18	.69

It will be seen that Common's and our results are somewhat parallel and seemingly opposed to those of Miller and Bearse. However, of Common's two birds, maintained on the wide ratio the heavy eater, and therefore on his regimen a heavy consumer of minerals, remained in positive balance and good health, whereas the poorly consuming bird, *i.e.*, with low consumption of minerals, ran a negative balance and failed in health. This complication of ratio with absolute quantity ingested has been extensively studied by Shohl (41) using rickets in rats as his criterion. This author shows that when a wider ratio is employed the absolute amounts ingested must be greatly increased if optimum results are to be expected. Siwe (45) has shown that the level of serum calcium and phosphorous is the significant factor as regards rickets in rabbits and not the Ca : P ratio. It seems likely therefore, that Miller and Bearse would have obtained results somewhat at variance with their present findings if they had been able to induce a heavier consumption of their inferior ration or had raised its levels of both CaO and P_2O_5 by about 50%. It is therefore highly probable that a normal ration such as ours containing 2% P_2O_5 or more will always require a heavy calcium consumption to be efficient. Where such heavy calcium consumptions are not secured, the phosphorus may well prove to be a limiting factor, and it might be profitable to investigate the possibilities of reducing the phosphorus content of normal poultry rations by limiting the use of high phosphorus ingredients such as fish meal and bone meal.

Calcium

Simultaneously with ovarian activity in birds there occurs a 200 to 300% increase in serum calcium. Hughes, Titus and Smith (25), Sun and Macowan (46), and Macowan (29). This increase is solely concerned with the undiffusible fractions, while the ultrafiltrable partitions remain unchanged, Correll and Hughes (16), Benjamin and Hess (3), and Taylor and Russel (47), or decrease slightly, Heller, Paul and Thompson (24). Siwe (43) showed that total serum Ca as well as its ultrafiltrate are lower in venous than in arterial blood. Further, that in normal subjects ultrafiltrable Ca has a tendency to remain stable irrespective of changes that may occur in total serum calcium. For instance, even intravenously injected Ca^{++} will appear in the serum as non diffusible calcium, Siwe (44), changes in the diffusible fractions occurring only subject to changes in the pH of the blood, Rana-Takahashi (36), Siwe (43 44). When parathyroid

hormone is added total serum Ca is slightly elevated, but with a greater rise in venous than in arterial blood. However arterial ultrafiltrate increases 100% more than the corresponding venous fractions with the result that the venous ultrafiltrate is only 60% of that in arterial blood. Added parathyroid hormone, therefore, not only mobilizes calcium from the bones but also acts on the blood calcium already present, Siwe (43). Clinical symptoms of calcium deficiency are hence not correlated to total serum calcium values, but to the level of their ultrafiltrates with unavoidable complications due to variability in individual reactivity, Siwe (42).

Halnan (23) fed his two birds a diet containing a total of 2.73% CaO or 4.88% $CaCO_3$. During egg laying periods the birds were allowed sufficient food to secure a steady ingestion of 41.0 gm. $CaCO_3$ per period of seven days. An analysis of the author's balance tables reveals a practically perfect correlation between the weight of eggs produced and the weight of negative or positive balance thereby induced. The regressions are linear and show that on this regimen one of his birds was able to produce about 240 gms. of eggs per period and the other 210 gms. Below these amounts positive balance was maintained, whereas any attempt to exceed these levels produced negative balance. Such attempts were made in one period by the least efficient bird and in three periods by the other. Sufficient draft on reserve stores was thereby effected to slow up the egg laying to such an extent that in the first instance production ceased before the end of the test and in the other instance was undoubtedly just about to cease. Common (14) showed, as mentioned previously, that a level of 5.54% $CaCO_3$ in the ration would just suffice to maintain a positive balance only on a high total food consumption, which would imply ingestion of comparatively large amounts of calcium. Common (15) further reported the observation that serum phosphatase values rose whenever egg laying was in progress, and fell with production pauses. In addition the phosphatase values were much lower on the above mentioned ration containing 5.54% $CaCO_3$ than on that having 0.66% $CaCO_3$, and with the latter there was 15% less ash in the fat free tibiae.

Oberling and Guerin (35) found that calcium restriction would induce hyperfunction of the parathyroid glands with consequent mobilization of osseous calcium, which, if persisted with, would result in chronic osseous disease. Low calcium diets have been shown by Guyatt, Kay and Branion (22), Mölgaard (34), Skil and Kay (40) and McGowan and Emslie (28) to produce osteoporosis; the latter authors found this condition accompanied by enlarged parathyroids. Gutman, Thyson and Gutman (21) showed this complex to be attended by the high serum phosphatase values reported by Common (15) in this author's above mentioned work.

In the calcium deficiency that may occur in fowls as a consequence of egg laying, the parathyroid, therefore, seems primarily stimulated to hyperfunction for the purpose of mobilization of bone calcium for egg shell formation. This assumption would satisfactorily account for the extraordinary phosphorus voidings preceding the laying of each egg, which was reported by Common (13) for birds maintained on low calcium diet and by Halnan (23) whenever egg laying in his birds proceeded at such a rate that demand for calcium exceeded supply. Furthermore, both authors

found that they could avoid this phosphorus elimination by maintaining the birds in positive calcium balance. A further argument in favour of this assumption is the above mentioned finding by Siwe (43) that added parathyroid hormone may act to maintain the necessary level of diffusible serum calcium, by mobilisation from the protein bound fraction. The enormous increase in the latter is probably a simple concomitant to the needed elevation of blood nitrogen in egg laying and at the same time a convenient store for mobilisable calcium.

These views would conclude in the conception that as long as birds are in positive balance, absorbed calcium from the gut will be found mainly in the protein bound fraction. From there it will be mobilised to the diffusible fractions and utilised through the glands of the uterus for egg shell. In negative balance, however, calcium is drawn from the bones with very little influence on total serum calcium but with strong attempts to maintain the necessary level of the diffusible fraction.

Against this view is the above mentioned finding by Common (15) that even in birds maintained on high calcium levels, the serum phosphatase rose and fell with egg production and production pauses respectively. Auchinachie and Emslie (1) doubted the value of phosphatase activity as an indicator of egg laying in normal birds, *i.e.*, birds in positive balance. It is true that the increases in egg laying from their twelve birds were by no means parallel to the increases in phosphatase values, but still there were increases for nine out of the twelve birds. However, the truth of the matter is, that as yet there is not sufficient data on which to form a sound conception of this complicated matter of calcium metabolism for egg production in fowls. For one thing, the important physiological variability in efficiency and balance, as stressed by Siwe (42) has not even been touched.

Typical decalification of bones was found in three of our groups of birds.

On November 1st, 1934, Group G, comprising 82 Barred Plymouth Rock pullets were placed in cages. These birds were fed the previously described ration with 1% cod liver oil and oyster shell *ad lib.* On March 14, 1935, all of these birds were removed directly from the cages to the killing floor. After killing and dressing, the carcasses were boiled and a clean separation of all soft tissues from the skeleton was attempted. This proved to be impossible, however, as the bones were found to be so "rotten" that thin flakes and sheets of bone came away when muscles and tendons were lifted off. The sternum, ilium, and ischium in many instances virtually crumbled away and the long bones were also affected. The sternal crest very frequently proved to be decalcified to such an extent as to be bent double on the antero-posterior axis, or the posterior point was telescoped. Trabeculae of the long bones were practically absent and the corticales were very thin and porous rendering these bones excessively breakable upon even slight pressure being applied.

Birds of groups A and C were treated in the same manner as those of Group G but with these 18 and 6 months respectively intervened between the time when the birds were released from the cages until they were killed. In all of these carcasses a perfectly neat and clean separation of soft tissues from bone was effected, as these skeletons were quite rigid and well calcified.

However, it was very plainly noticeable that a similar condition of decalcification had previously obtained. The recalcification of the bones from Groups A and C may have come about as a natural consequence of the pause in egg laying during the moulting season, and the subsequent diminished draft on calcium with second season lowered production. However, there is also the possibility that the cage environment might in some way restrict the free ingestion of calcium below the adequate quantitative level, or that the utilisation of ingested amounts of calcium is somehow interfered with under this environment.

For the purpose of obtaining estimates of the level of oyster shell consumed by our birds in relation to their output of calcium, the paired observations on weekly total weight of egg production, and of ingested weight of oyster shell were plotted for random samples of birds from Groups A, B, C, E, and G. From the plotted diagrams were determined the mean production values for each oyster shell consumption class. The curves thus obtained are plotted in Figure 3.

Analyses in our files show that there is approximately the same percentage of $CaCO_3$ in oyster shell and in normal egg shell. A fairly good estimate of the balance between ingested calcium and that voided as egg shell may be arrived at by comparing the calculated weight of egg shell produced with the amount of oyster shell consumed in a given period. The ratios, oyster shell consumed to egg shell produced, were therefore calculated from the two mean values characteristic of each determinative point in the curves and the figures denoting these ratios are affixed to the points of the curves in the chart. The frequency polygons for numbers of determinations, or weeks per oyster shell class, are superimposed on the correlation curves. The mean number of determinations in each polygon is also indicated.

It may be seen from this graph that in a large proportion of the weekly determinations the birds consumed less than or barely sufficient calcium to cover their need for egg shell. It is also noticeable that the optimum ratios for high production ranged between 2.25 : 1 and 2.84 : 1. This fits remarkably well with the findings by Sherman (39) for humans. This author states: "The optimum level of calcium intake is about three times as high as the minimal adequate level which meets the directly demonstrable requirements———." During egg laying periods in which the weight of production was similar to optimum for our birds, Halnan's birds eliminated calcium in droppings that tended to assume the same values as that voided as egg shell. However, these birds were in all such periods in negative balance, as mentioned above, and therefore under stress of eliminating as small amounts of calcium in droppings as possible. Fairbanks and Mitchell (19) showed for rats, that the percentage utilisation of calcium is inversely proportional to the percentage calcium in the ration. Furthermore the regression that may be plotted from the data of these authors is curvelinear conforming to a characteristic curve for diminishing returns. It is obvious that a quantitative calcium restriction in the ration will induce a very much stricter economy than would a more liberal ration which was designed to preserve a positive balance. On such a ration the elimination of droppings calcium would therefore be enlarged by an in-

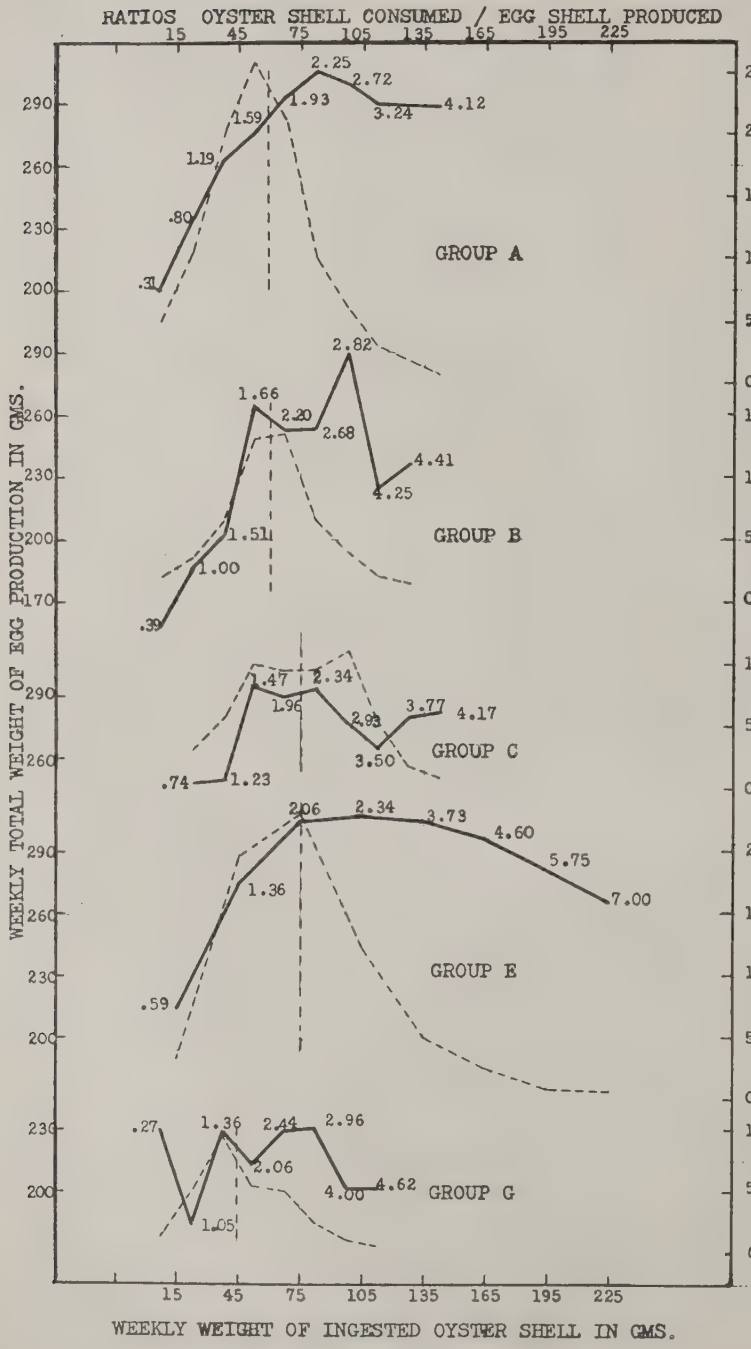
RATIOS OYSTER SHELL CONSUMED / EGG SHELL PRODUCED
15 45 75 105 135 165 195 225
WEEKLY TOTAL WEIGHT OF EGG PRODUCTION IN GMS.
NO. OF WEEKS PER OYSTER SHELL CLASS
GROUP A
.31 .80 1.19 1.59 1.93 2.25 2.72 3.24 4.12
GROUP B
.39 1.00 1.51 1.66 2.20 2.68 2.82 4.25 4.41
GROUP C
.74 1.23 1.47 1.96 2.34 2.93 3.50 3.77 4.17
GROUP E
.59 1.36 2.06 2.34 3.73 4.60 5.75 7.00
GROUP G
.27 1.05 1.36 2.44 2.96 2.06 4.00 4.62
WEEKLY WEIGHT OF INGESTED OYSTER SHELL IN GMS.

FIGURE 3

creasing ratio to the increase in consumption. On analysis of Halnan's figures this is exactly the situation which pertains. On a curvelinear regression it is found that when weight of production is lowest, and therefore the calcium supply most liberal, the calcium in droppings rises to twice that voided as egg shell. It may be assumed, therefore, that ratios such as those revealed by Figure 3 to be characteristic for optimum production are true optima as far as the physiological state of the birds is concerned.

It may be seen from Figure 3 that mean optimum production occurred in weeks in which mean oyster shell consumptions ranged between 85 and 105 gms., or roughly 80 to 100 gms. $CaCO_3$. Comparing an average of 90 gms. with Halnan's 41 gms. weekly consumption, which represented 4.88% $CaCO_3$ of the total consumption, it may be assumed that about 10.7% $CaCO_3$ in the ration will be optimum for a weekly production of approximately 300 gms. of eggs.

A covariance was calculated for birds of Group C, correlating egg production to the percentage oyster shell in the weight of mash consumed in such weeks wherein the oyster shell to egg shell ratio was 2 : 1 or higher. The result is presented in Table 7.

TABLE 7.—COVARIANCE OF PRODUCTION TO PER CENT OYSTER SHELL CONSUMED

	D.F.	X Egg production		Y Per.cent shell		Covariance		
		Σ sq.	Mean sq.	Σ sq.	Mean sq.	Σ prod.	r	b_{yx}
Between hens	16	212,768.4		397.8		2136.4		
Within hens	142	442,616.7	3117.0	769.9	5.4	9572.5	0.519	0.022
Total	158	655,385.1		1167.7		11708.9		

The mean percentage oyster shell in total feed amounted to 10.2% through these 159 weeks, and the mean weight of production was 231.6 gms. The regression is 2.2% oyster shell per 100 gms. production, and for a weekly production of 300 gms. optimum oyster shell consumption should therefore be 11.7% or 11.1% $CaCO_3$ in the total ration. There is thus good agreement between the results of the two methods by which the optimum percentage oyster shell in total ration is calculated.

It is obvious that fowl will not be able to draw indefinitely on their calcium reserves for any length of time and yet continue life as normal birds. If, therefore, the calcium intake is too low for the protection of tissues and for normal egg production, the result will sooner or later be a slowing up or complete cessation of egg laying. Buckner and Martin (5) and Buckner, Martin and Peter (6, 7, 8, 9, 10) have described the fate of chickens maintained in a state of calcium restriction. They state that such restriction limits production of eggs and deposition of calcium on the shell membranes, that it depletes body material (phosphorus, fat and nitrogen) and causes decrease in vigour with adverse effect on fertility and hatchability, and that egg laying may continue till there is a general depletion

of the bones in magnesium, phosphorus and calcium. It is a curious fact that our birds during the majority of weeks, in spite of unlimited access to oyster shell consumed such small amounts as to place the severest handicap on their uninterrupted formation of normal eggs. The character and extent of this self-imposed limitation is well illustrated in Table 8.

TABLE 8.—COMPARISON OF PER CENT PRODUCTION TO PER CENT WEEKS AT OPTIMUM Ca INTAKE

Group	B	A	E	C
Production	47.4	58.0	59.0	61.8
Weeks at or above optimum Ca intake	13.8	21.0	32.0	50.0

In this connection it is interesting to note that in every instance wherein a pause, a moult, or a broody period occurred, they were preceded by periods of low oyster shell consumption. Riddle, Bates and Lahr (37) and Bates, Lahr and Riddle (2) showed that atrophy of ovary with cessation of laying followed by broodiness were the results of intramuscular injection of their "Prolactin" preparation of the anterior pituitary gland into actively laying fowl. The mechanism of release of the hormone into the blood stream is not yet known, but as an atrophic ovary appears to be a necessary precursor for the specific action of the hormone it becomes highly probable that the hormone is always present in physiological amounts in the blood stream, or is released from the pituitary in response to the atrophic ovary. It seems possible therefore that the mere fact of preventing the slowing up of egg laying through calcium restriction might act as a non specific for the elimination of broodiness.

It has been mentioned previously that in many of our caged individuals there was exhibited an extreme nervous irritability. Massengale (27) commented on the nervousness in the birds which he maintained on low calcium diets. Chang, Shafer, and Gerard (12) found that small increases or decreases in calcium had a marked inverse influence on nerve respiration and irritability, Gerard and Magoun (20) showed a consistently decreased nerve reaction to Ca^{++}, and Duckworth and Godden (17) reported violent nervous reactions to the binding of serum calcium by citrate ions. In the light of these observations it seems wholly plausible that the slight lowering of the ionized fraction of serum calcium in laying hens, which has been noted by some authors and not by others, may, where it does occur, be due to calcium restriction, and may cause the higher nervous irritability noted both in Massengale's and in our birds.

There can, however, be little doubt, that the self-imposed restriction in calcium intake has been, if not entirely at least to a major extent, responsible for the severe limitation imposed upon the full expression of the inherent ability for egg laying in our caged birds. Whether the caged environment imposes a direct restriction in the quantity of oyster shell ingested, or whether this environment also interferes with absorption and utilization cannot yet be decided. This and other phases of the problem are under investigation.

SUMMARY

1. Egg laying by groups of individually caged birds is attended by 25% lower variability than that characteristic of groups under normal environment.

2. This lower variability is obtained by reduction in both the low and the high "tails" of the distributions, as well in extent as in number of observations.

3. Caging therefore acts as a limitation towards the production of high records and beneficially on the freer expression of inherent fecundity in physically poorer birds.

4. Hatching results may sometimes be entirely subnormal under this environment.

5. It is possible that the high phosphorus content of "normal" poultry rations constitutes a limiting factor in egg production and health.

6. It is shown that caged birds in the majority of weekly periods consume wholly inadequate amounts of oyster shell to provide for their egg shell and faeces voidings of calcium. They therefore draw on bone reserves, resulting in abnormal bone condition and restriction or pause in egg laying. A pause in egg laying may be the forerunner of broodiness. Calcium restriction may produce nervous irritability.

It is shown that about 11% $CaCO_3$ in the total ration is required to maintain a production of 300 gms. of eggs per week and at the same time protect the skeleton.

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Résumé

L'effet de la réclusion sur la fécondité et l'aptitude des volailles à la reproduction. S. Bird, Service de l'Aviculture de la Ferme expérimentale centrale, d'Ottawa

Les poules tenues individuellement dans des cages séparées ont une ponte plus uniforme, par groupe, que celles qui courent en liberté dans des parquets. La ponte n'atteint jamais un point aussi élevé que chez ces dernières ni ne descend à un point aussi faible. Les écarts, en plus ou en moins, ne sont pas aussi prononcés. La variation est de 25 pour cent moins forte. La réclusion en cage suppose donc à la production de très grosses pontes, par contre, elle donne aux oiseaux moins vigoureux l'occasion de mieux démontrer leur fécondité inhérente. Dans ces conditions, il peut arriver que les résultats de l'éclosion soient entièrement subnormaux. Il est possible que la haute teneur en phosphore des rations "normales" soit un facteur limitatif dans la production des œufs et dans le maintien de la santé des volailles. Il est démontré que dans la majorité des périodes hebdomadaires, les sujets en cage consomment des quantités tout à fait insuffisantes de coquilles d'huîtres pour couvrir le calcium contenu dans leurs coquilles d'œufs et évacué dans leurs fientes. Ils tirent donc sur les réserves d'os, et il en résulte un affaiblissement des os et une restriction ou un arrêt de la ponte. Cet arrêt de la ponte peut être un avant-coureur de la fièvre de couver. La restriction de calcium peut produire une irritabilité nerveuse. On a constaté qu'il faut environ 11 pour cent de $CaCo_3$ dans la ration totale pour maintenir une production de 300 grammes d'œufs par semaine et, en même temps, protéger le squelette de l'oiseau.

INHERITANCE OF EGG PRODUCTION IN THE DOMESTIC FOWL

II. INCREASES IN PRODUCTION, THEIR EXTENT AND CHARACTERISTICS WITH A DISCUSSION OF CAUSAL FACTORS[1]

S. S. Munro[2]

Dominion Experimental Farm, Ottawa, Ontario Canada.

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In the preceding paper of this series (3) an attempt was made to show the very complex nature of the mechanism governing the egg producing potentialities of the domestic fowl. Attention was drawn to some underlying laws governing the distribution of Mendelian populations, and the direction, rate and characteristics of a genetic change due to selective breeding on the distribution of a population was discussed. By means of a comparison of actual data with theoretical expectation, it was concluded that non-genetic influences were responsible for the majority of the variance in a population. It was further pointed out that genetic variation under one environment might become obscured or even reversed under a second. The methods of selection largely followed by poultry breeders in attempts to improve the egg laying ability of their birds, would seem, in view of the complexity of the problem, to give little assurance of pronounced success.

In contrast to this expectation, the average yearly egg production of the surviving Barred Plymouth Rocks in Canadian Egg Laying Contests increased from 131 eggs in 1919–20 to 199 eggs in 1934–35. During this time rather extensive phenotypic selection has been practised on the female side and the increase in production is commonly attributed to this.

In this paper, the characteristics of the contest population curves during the years when the mean production was rising will be compared with those to be expected if the increase was genetic in nature. In this way, additional evidence concerning the causal nature of increased production may be secured. By egg production, in this paper, is meant annual egg numbers; no reference to egg weight is intended.

The contest records have been used in this study because it is felt that they reflect the genetic status of flocks in the country at large more accurately than would data from private or institutional flocks. Any conclusions drawn in this paper do not apply specifically to any single policy or breeding project. Methods of breeding in general are under discussion.

CHARACTERISTICS OF GENETIC IMPROVEMENT

Among the changes which occur when efficient selection is practised and which were dealt with in the preceding paper are:—

1. A shift in the mean of the population in the desired direction. This shift or increase in the mean is greatest in the first generation of selection

[1] Contribution from the Division of Poultry Husbandry.
[2] Graduate Assistant, Poultry Division.

and although it continues, it does so at a diminishing rate in each succeeding generation.

2. A corresponding decrease in the standard deviation, greatest in the first generation of selection and continuing at a diminishing rate in succeeding generations.

3. A corresponding increase in skewness in the curve of distribution, which is greatest in the first generation of selection and likewise decreases in rate in succeeding generations.

DATA FROM EGG LAYING CONTESTS

In Table 1 the mean production of the surviving Barred Plymouth Rocks is given for the fifteen years used in this study together with the corresponding standard deviations and mortality rates. The means are plotted in Figure 1. In the year 1932–33 those birds which had not laid sufficient eggs by the end of the 37th week to give them a chance to reach the 200 egg mark by the end of the 51st week, were returned to their owners. The mean for that year is estimated on the production to the end of the 37th week. No standard deviation or death rate is shown for this incomplete year.

FIGURE 1.—Mean production of the Barred Rocks in Canadian Egg Laying Contests east of B.C., by years.

Table 1 and Figure 1 show that, in general, the first of the listed characteristics of genetic improvement has occurred, *i.e.*, the mean has moved in the desired direction, its rate of increase being greatest during the first few years and, in general, diminishing in succeeding years. However, when one considers that new breeders, many of whom did not practise trapnesting, were entering each year, that the proportion of birds from selected parents varied from year to year, and that, especially in the early years, relatively few birds were the results of one or more generations of selective breeding, it would appear that the rate of increase is much too rapid and consistent in these years to be due entirely to selection.

A decrease in the standard deviation, the second characteristic of genetic improvement, does not occur as can be readily seen by referring to Table 1. In fact each of the first two years have lower standard deviations than any subsequent year.

TABLE 1.—NUMBER OF SURVIVORS, MEAN PRODUCTION, MORTALITY LEVEL, AND STANDARD DEVIATION FOR THE BARRED PLYMOUTH ROCKS IN ALL EGG LAYING CONTESTS IN CANADA, EAST OF B.C., BY YEARS

	1919–20	1920–21	1921–22	1922–23	1923–24	1924–25	1925–26	1926–27	1927–28	1928–29	1929–30	1930–31	1931–32	1932–33	1933–34	1934–35
No. of survivors	507	814	795	962	1,082	1,096	1,041	1,211	1,217	1,272	1,340	1,348	1,240	—	1,313	1,178
Mean production	131.1	142.4	158.2	169.3	173.5	170.1	181.9	178.4	181.9	189.7	187.8	188.8	191.5	196.0	194.1	199.0
Mortality %	9.3	11.8	14.7	13.2	14.6	12.0	12.9	17.0	18.0	16.2	18.8	26.4	24.8	—	20.5	20.0
Standard deviation (eggs)	42.0	44.8	52.2	48.5	47.7	47.5	48.7	47.5	46.6	46.6	45.5	48.5	45.6	—	45.6	44.7

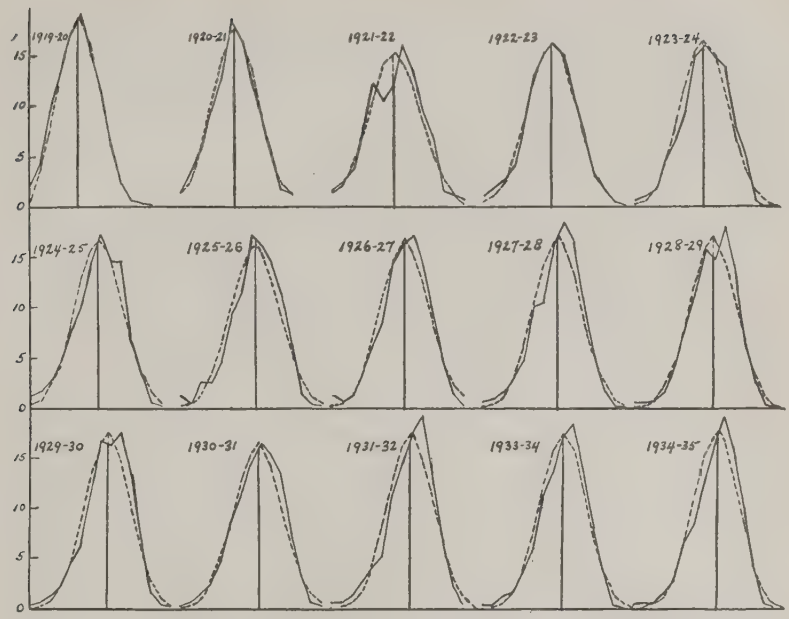

FIGURE 2.—Solid line: frequency polygon of Barred Rock contest populations by years. Broken line: best fitting normal curve.

With regard to the third point, that of skewness, it can be seen in Figure 2 that the distribution curves for each of the fifteen years conform very closely to the normal curve. While application of the X^2 test for goodness of fit, reveals that, beginning with the year 1924–25 the curves differ significantly from normal, and inspection of Figure 2 shows that this is chiefly due to skewness, it can be seen that the skewness which does exist is far smaller than that which would be expected if the increase of approximately 70% which has occurred during these 15 years was due entirely or largely to genetic improvement. In addition to this there are other factors which must be borne in mind and which, undoubtedly, contribute to the skewness.

In the first place, the normal curves which have been superimposed over the observed distributions in Figure 2 are calculated on the basis of the observed standard deviation which, in each case, includes the individuals forming the low left tail of the curve. While this low left tail which characterizes most of the curves may be due in part to the genetic segregation of low individuals, there is little doubt that a goodly portion is caused by abnormal individuals such as birds which lay a few eggs and then ovulate intra-abdominally, and those which after beginning to lay are seized with some pathology which interferes with or prevents further egg laying. These birds overlap the genetically poor layers and, in the absence of definite criteria for differentiation, are indistinguishable in the records. The inclusion of such birds in the population causes the calculated normal

curve to be slightly broader and with a lower mode than the observed distribution. It also has a tendency to lower the mean of the actual population and this places the normal curve slightly to the left of its true position. Inspection of Figure 2 reveals that a slight narrowing and heightening of the normal curve accompanied by a slight shift to the right will produce a closer fit to the observed distribution.

A second factor contributing to the skewness is the fact that the majority of the deaths occur among the poorer layers as shown by Munro (2). This selective mortality removes from the original population, through mortality, more birds below the mean than above it and consequently flattens the left side of the curve. It also tends to increase the mean and is probably a factor of some consequence in determining the mean production, especially since the year 1926–27 when the death rate has been consistently above 15%.

THE PART PLAYED BY GENETICS

The foregoing discussion suggests that selective breeding may have played a rather small part as a causal factor of increased production. It is difficult to evaluate definitely or even approximately the part played by inheritance, and it is perhaps dangerous to suggest that its part has been insignificant. In fact, it is not intended to deny that breeding has been responsible, to some extent, for the high egg laying potentialities of the modern hen. The point this paper is concerned with is simply to point out that the increase which has occurred in the mean production of the Barred Plymouth Rocks entered in Canadian Egg Laying Contests, since these contests began, appears on critical analysis to be due, in the main, to non-genetic causes.

That the increase which occurred during the first three years of the contest could not reasonably be expected to be due to breeding is admitted by the contest management as evidenced by the following quotations taken from the official report of the first three years (1),—"Since the breeding of qualified contest birds could not have had any effect on the second year's birds as they were entering when the 1919–20 contest birds were leaving the contests and since production improvement is transmitted very largely through the male, the female progeny of the first contest females are the only ones that could favourably affect production in the third series of contests, and as the number of these pullets was very limited one cannot reasonably expect that the influence created by them was sufficient to account for the increased egg yield. It cannot be denied that the management of the laying contest has improved each year, that the feeding practice has been more carefully studied and administered, that more capable poultrymen have been employed in the carrying out of every detail, but any or all of the above improvements are not, we believe, responsible for the decided improvement which has taken place. More careful selection of the contest pens was the major factor in the improvement shown from year to year. Contestants soon learned that there was a difference in the way pullets performed after entering the contest and that age of bird (or better development of bird) was a very important factor. They soon learned that the proper development was just before the birds started

laying, and this one point in selection has been the means of getting breeders to pay greater attention to the hatching of their contest birds. A decided improvement has been noted in this regard, and we believe has exerted as much influence as any other factor."

These first three years as can be seen by referring to Figure 1 show the greatest increase over previous years. The rate of increase from year to year thereafter, when the results of selective breeding would be expected to play any part they might be destined to play, is smaller. This in itself, without supporting evidence, appears to be sufficient to show that non-inherited factors play a greater part than do inherited ones.

In addition to the non-genetic causes recognized by the management and which applied particularly to the first few years, there are others which played a very significant part in later years. Before mentioning these, there is a situation in connection with any small genetic improvement which may have occurred, which should be mentioned.

There is, on the whole, little doubt but that individuals and families differ in their inherited ability to produce eggs. These differences often become obscured due to gene-environment interactions, as explained in the preceding paper, and one has difficulty in distinguishing genetic differences, in the great majority of cases, even by the progeny test. Eventually, however, through chance recombination of genes a particularly prepotent individual, male or female, will occur which is capable of transmitting to his or her daughters an egg producing ability which is definitely and consistently higher than the average. When the prepotent individual is a female, the limited number of daughters produced makes the prepotency difficult to recognize and, if recognized, the limited offspring which can be produced in any one breeding season comprise but a small part of the flock and have a proportionately limited effect in raising a flock average. When, however, the prepotent individual is a male, its effect is more apparent since it is not uncommon for a male to have 100 or more daughters. When one or more pens of daughters from such a male are entered in egg laying contests, the attention of poultry breeders is focused upon these birds, and their owner receives more than his usual share of orders for hatching eggs, baby chicks, and breeding stock. Cases have been known where such a male was bred for two or three seasons, his daughters either winning or standing close to the top each year. The owner, in the meantime, extensively sells the male's progeny (either 1st or 2nd generation). The blood of such a male in this way becomes more widespread than it otherwise would. The history of contest work shows that the breeder who earns a reputation for a few years as a producer of high-laying stock soon drops back until his birds are no better than the average. This is probably due to the gradual dilution of the prepotent male's blood until it ceases to have an appreciable influence on the flock as a whole. Demand for stock falls off accordingly and the majority of purchases are being made as usual from the breeder with the current reputation.

It seems likely, therefore, that what small amount of genetic improvement has occurred and likewise what little genetic skewness does actually exist is probably due as much to the psychology of the buyer as to the method of selection practised by the breeder.

HISTORY OF PRODUCTION BREEDING

Twenty-five or more years ago, trapnesting as a basis of selective breeding for egg production was pretty much confined to an occasional institution. Trapnesting on private plants was done chiefly by exhibition breeders desirous of improving the show quality of their stock. The general farmer kept a few hens to supply the household and perhaps a few to market in the season of flush production. The birds were, as a rule, poorly housed and poorly fed, foraging largely for themselves in the summer and being fed mostly on the lower grades of home grown grains. Exhibition breeders, mostly back-yard fanciers, spent considerable time at their hobby and their birds were generally supplied at certain seasons of the year at least, with "conditioning feeds", chiefly protein in nature such as fresh meat, or dried animal or vegetable concentrates. In spite of the fact that these birds were often closely inbred and unselected for egg production, it is not surprising, in view of the care in feeding and management, that exhibition birds were comparatively good layers and often excelled the average farm bird in egg production. Estimates of the average egg production of the farm hen were secured in census returns and were necessarily inaccurate, the error being on the low side mainly for the reason that farmers generally fail to realize the number of eggs which do not leave the farm, being used in the household, for hatching purposes, lost due to stolen nests, etc.

Attention, however, soon became focused on breeding utility birds for egg production, probably due to the results obtained by Pearl at Maine where marked improvement in egg production was secured by a strict progeny test method of selection, after selection on pedigree and performance over a period of nine years had failed to produce results. Goodale at Massachusetts also secured marked results with the progeny test.

In Canada, trapnesting for the purpose of improving egg production became general in governmental institutions shortly after the beginning of the century. During the second decade it became fairly widespread and was adopted by numerous private breeders. During the year 1918–19, the first egg laying contest sponsored by the Dominion government was conducted at Charlottetown, P.E.I. By 1919–20, contests were being conducted in every Canadian province.

By the year 1921–22, there were in operation in Canada several breeding policies all being sponsored or officially recognized by the Dominion government, all having as their objective improved egg production combined with standard characteristics and all having the same fundamental basis of selection or recognition of the desirable future breeders. These policies included Record of Performance "A", Advanced Record of Performance "A", Record of Performance "AA", Advanced Record of Performance "AA" and Registration.

Officially recognized birds were, in each case, females not otherwise disqualified which produced a certain set minimum number of eggs within a given time limit, usually 51 or 52 consecutive weeks. In some of the policies the grade and weight of the egg was taken into consideration.

These various official channels for the recognition of superior laying females were set up as a means of regulating the bred-to-lay poultry industry and of eliminating the false advertiser. The poultry industry

received a tremendous stimulus and so called bred-to-lay birds were in great demand. Average production per bird rose rapidly as is indicated in Figure 1 and it was but natural that credit for this should be laid chiefly at the door of selective breeding, even though at the same time considerable improvement was being made in feeds and feeding methods as well as general management practices.

NON-GENETIC IMPROVEMENTS

By the time R.O.P. and Contest work started considerable improvement had already been made in feeding practices. Chief among these was undoubtedly the addition of protein concentrates such as meat and bone meal to the ground grains or mash and the feeding of liquid whole or skim milk. These animal proteins in addition to increasing the protein level, supplied proteins from animal origin and thus added variety to the amino acids, a point which, at that time, may not have been fully appreciated by poultrymen. The bone meal and milk also supplied needed minerals, particularly calcium which is required in such large quantities by the laying hen. The contest birds were also kept in more comfortable and less crowded quarters than the average farm bird, particularly in the winter months when confinement was necessary. Undoubtedly, however, the improvements in feeding were mainly responsible for the extent to which the first contests exceeded the farm flocks. Private breeders who had taken an interest in breeding for egg production had made similar improvements in feeding practices. Interest in production birds, to the extent of keeping trapnest and pedigree records, was invariably accompanied by improved feeding and management practices. Unfortunately, even at responsible institutions very little or no control on the effects of breeding *vs.* environment was available, in that no unselected, random breeding flock was maintained under similar improved conditions. Comparisons were made entirely between production in the current year under current conditions with that made in past years under past conditions.

After the beginning of contest work, during the years covered by the data presented in this paper, further notable improvements continued to be made in feeding practices. Among these may be mentioned the incorporation in feeds of powdered milk and fish meal which latter was much improved by being manufactured from white fish and being rendered fat free or nearly so. Another important step was improvement in the quality of meat scraps, in that less offal, hoof and horn was placed therein and better quality protein was insured by using a wider variety of organs and tissues, thereby increasing the kinds of amino acids, the essential nature of some of which was becoming fully recognized; in fact the increasing use of meat scrap in poultry feeds led several companies to manufacture this product especially for poultry. The discovery and incorporation of vitamin D in the ration, chiefly in the form of cod liver oil, was perhaps the biggest improvement since the addition of protein concentrates to the mash. Previous to the use of cod liver oil in the ration, it was found practically impossible to rear chicks indoors since they invariably developed rickets. The use of cod liver oil eliminated this trouble and also played a most important part in supporting winter egg production. In later years

biological testing and standardization of cod liver oil has greatly improved its efficiency. The value of vitamin A in poultry nutrition has also only been fully appreciated in recent years and as a result more attention is being paid to the standardization of this essential; the incorporation of alfalfa leaf meal in the mash, chiefly as a source of vitamin A, is of considerable benefit to laying birds especially in the season of close confinement.

These advancements in feeds are perhaps the chief contributing factors to high egg production but they do not constitute by any means all these factors. Improvements in housing and management have played a part. This is particularly true, so far as the contests are concerned, in the first few years. The development of poultry houses chiefly in the direction of providing greater warmth and comfort in the winter months and the employment of more capable poultrymen, especially better feeders, have each made significant contributions.

Any discussion of factors contributing toward high egg production would not be complete without mentioning improvements in disease control and prevention. Only a decade ago, the first three weeks in the life of a chick were considered the most critical. The majority of deaths occurred during this period and it was not uncommon for mortality to run as high as 25 or 30%. At the present time mortality during this period on well managed farms rarely exceeds 5%. This improvement is mainly due to the eradication of pullorum disease from the breeding stock through blood testing. This disease is carried in the ovaries of infected hens and passed through the egg to a proportion of the chicks, whence it rapidly spreads to healthy chicks. It is generally admitted that the egg producing ability of infected individuals is impaired and since there are far fewer infected individuals in laying pens to-day than 10 or 12 years ago, egg production has benefited correspondingly. As a matter of fact, in recent years, all birds must be blood tested and reactors eliminated before entering contests. Much progress has also been made in reducing parasitic infections with a corresponding gain in egg production.

While it is true that new diseases continue to appear and that the older ones are still prevalent, in fact the disease situation appears to be more acute each year, the above examples are mentioned to show that progress has been made and that certain pestilences have been largely brought under control without which present day losses in egg production would be greater than they are.

All in all these various improvements when spread over a period of years, seem quite sufficient to account for most of the increased production illustrated in Figure 1.

Again the writer should like to point out that no specific criticism of Contest, Registration, R.O.P. or other individual or co-operative project is intended. What appear to be facts are presented and discussed. The data in this paper have been derived from contest records simply because they are representative of the country as a whole and because they were convenient to access for purposes of this study. Further papers in this series will be more technical in nature and will deal in detail with pedigree records from other sources.

SUMMARY

1. Data from Barred Plymouth Rocks entered in Canadian Egg Laying Contests between the years 1919 and 1935 are presented and the means, variabilities and characteristics of the distribution curves are compared with those expected if the observed increase in mean production per bird were due to selective breeding.

2. This comparison indicates that most of the increased production during that period is due to other than heritable causes.

3. Non-genetic causal agents are reviewed and it appears that they are quite sufficient in extent of both variety and effect to account for most of the increase.

4. The precise amount of the increase which can be ascribed to genetic improvement is difficult to estimate. It is perhaps best to say that the increase which has occurred in the production of the average Canadian hen since trapnesting and individual pedigreeing became widespread is mostly due to improvements in feeding and management, and that the amount of this increase which is the result of breeding work is far smaller than is commonly supposed.

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Résumé

Transmission héréditaire de la ponte chez les volailles domestiques. II. Augmentations de production, leur importance et leurs caractères, et analyse des facteurs qui les causent. S. S. Munro, Ferme expérimentale fédérale, Ottawa.

Les données relatives aux poules Plymouth Rocks Barrées inscrites aux Concours canadiens de ponte entre les années 1919 et 1935 sont présentées dans cet article, et les moyennes, les variations et les caractères des courbes de distribution sont comparés avec ceux auxquels on pourrait s'attendre si l'augmentation constatée dans la production moyenne par oiseau était due à l'élevage scientifique. Cette comparaison indique que la plus grande partie de la production croissante pendant cette période est due à d'autres causes qu'à des causes héréditaires. L'auteur passe en revue les agents causatifs non-génétiques et il semble qu'ils sont tout à fait suffisants par leur variété et par leur effet pour expliquer le plus gros de cette augmentation. Il serait difficile d'évaluer le montant exact d'augmentation qui peut être attribué à l'amélioration génétique. Peut-être est-il préférable de dire que l'augmentation qui s'est produite dans la production de la poule canadienne ordinaire depuis la généralisation du contrôle au nid-trappe et de l'enregistrement individuel, est due en grande partie à la meilleure alimentation et aux meilleurs soins et que la proportion de cette augmentation qui est le résultat de l'élevage est beaucoup plus faible qu'on ne le suppose communément.

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THE INHERITANCE OF EGG PRODUCTION IN THE DOMESTIC FOWL

III. DIFFERENCES IN TRANSMITTING ABILITY OF DAMS, AND THE DEGREE OF DAM-DAUGHTER CORRELATION[1]

S. S. Munro[2], S. Bird[3] and J. W. Hopkins[4]

Dominion Experimental Farm and National Research Laboratories, Ottawa, Canada

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Attention has already been called to the divergence of view among poultry geneticists and practical breeders respecting not only the mechanism of inheritance, but also the methods of breeding for increased egg production. In the first paper of this series the problem was considered theoretically, and it was maintained that inheritance played only a minor part in individual bird variation. In the second paper, the increase which has occurred in the egg laying ability of the hen since the beginning of the century was discussed. A consideration of the characteristics of improved production as exemplified by contest data indicated that the modern hen owes her egg laying ability chiefly to improvements in feeding methods and other management practices.

In this paper, egg production records from individually pedigreed flocks will be examined in some detail in an effort to secure additional information on the rôle of genetics in determining laying ability.

SOURCE OF DATA

With the co-operation of the Assistant Dominion Poultry Husbandman, egg production and egg weight records were secured from seven Dominion Experimental Farm flocks in Eastern Canada. These consisted of the first-year laying records of 1,165 pedigreed Barred Plymouth Rock pullets. Flocks were chosen in which only normally matured pullets had been placed in the laying house, and in which little subsequent culling had occurred during the pullet year other than the occasional removal of a bird characterized by a standard disqualification or some gross anatomical abnormality. Presumably such removals did not interfere with the unselected nature of the original populations with respect to egg production, but since complete yearly egg records, only, were used in the study, any relationship existing between production and mortality in individual birds would introduce an element of bias. It should also be pointed out that the data employed have been drawn entirely from flocks in which all females used as breeders laid 200 eggs or more during their first production year. This selection of breeding dams is consistent with the practice universally adopted in breeders' flocks at the present time. The variation which characterizes our populations may therefore be presumed to be typical of that which will occur in unculled "bred-to-lay" pullet flocks.

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[1] Contribution from the Division of Poultry Husbandry.

[2] and [3] Poultry Division, Experimental Farm, Ottawa.

[4] Division of Biology and Agriculture, National Research Laboratories, Ottawa.

THE TRANSMITTING ABILITY OF DAMS

It was decided first to test by means of an analysis of variance whether individual dams did differ significantly in their transmitting ability. The yearly egg production of the pullets from each farm were therefore tabulated according to sire, and the progeny of each sire grouped according to dam. The total variance of the offspring of each sire was analysed into a portion representing differences in the average production of the daughters of different dams, and a remainder representing the variation between daughters of the same dam. Results for the individual males were then pooled by adding degrees of freedom and sum of squares from each male, and an analysis of variance was thus secured for each farm. A further pooling of the entire data was effected by adding the degrees of freedom and sums of squares from each farm. Snedecor's (4) table of F was used to test the significance of the differences between dams. Table 1 shows the analysis of variance of yearly numbers of eggs for the progeny of a typical sire (Central Experimental Farm sire No. 676); Table 2 shows the combined analysis for all sires on the C.E.F. in 1932; Table 3 shows the combined results from all seven farms. Detailed data from which these tables are derived are on file in the Poultry Division, Central Experimental Farm, Ottawa.

TABLE 1.—ANALYSIS OF VARIANCE OF EGG PRODUCTION OF THE PROGENY OF C.E.F. MALE NO. 676

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F	Necessary value of F for P. of 0.05
Total	12	21,927	1,827		
Between dams	4	10,960	2,740	2.00	3.84
Within dams	8	10,967	1,371		

TABLE 2.—ANALYSIS OF VARIANCE OF EGG PRODUCTION OF PROGENY OF TEN MALES AT THE C.E.F. 1932. AVERAGE DIFFERENCES BETWEEN MALES EXCLUDED

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F	Necessary value of F for P. of 0.05
Total	127	222,348	1,751		
Between dams	30	79,183	2,639	1.79	1.98
Within dams	97	143,165	1,476		

TABLE 3.—ANALYSIS OF VARIANCE OF EGG PRODUCTION OF PROGENY OF SIXTY MALES FROM ALL FARMS. AVERAGE DIFFERENCES BETWEEN MALES AND LOCATIONS EXCLUDED

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F	Necessary value of F for P. of	
					0.05	0.01
Total	1,105	1,804,589	1,633			
Between dams	214	472,070	2,206	1.47	1.03	1.04
Within dams	891	1,332,519	1,496			

Table 3 shows that there were, on the whole, significant differences in the average production of the daughters of different dams mated to the same male. These differences in the average transmitting ability of dams were small in general, and, except in large groups, do not attain the level of significance. It would seem, therefore, that genetic differences between families did exist, but played a relatively small part in determining the total variation of the flocks. These data, therefore, support the conclusions tentatively arrived at through the application of genetic theory to the problem.

That the differences between dams were slight and inconsistent is well illustrated by the fact that at two farms, Fredericton and Harrow, half sisters were more nearly alike on the average than full sisters (Table 4). In other words, in these instances maternal inheritance was ineffective in causing significant differences between pullets from the same sire but out of different dams. Therefore, selection of pullets on their individual record, or even of dams on the progeny test basis at either of these two farms during the year 1931–32 would have been fruitless.

TABLE 4.—ANALYSIS OF VARIANCE OF EGG PRODUCTION AT THE TWO FARMS WITH THE HIGHEST AVERAGE PRODUCTION PER BIRD

	Fredericton		Harrow	
	D.F.	Mean square	D.F.	Mean square
Total	144	1,125	174	2,530
Between dams	28	850	30	2,459
Within dams	116	1,192	144	2,544

In this connection it is of considerable interest to note that these two farms have the highest average egg production and therefore, presumably, the most nearly optimal environment. One might ordinarily expect that under these conditions genetic differences between families could be discerned more clearly and accurately than under less favourable conditions. As a matter of fact, exactly the reverse appears to be true. Table 5 shows the mean production and F value or number of times the mean square between dams exceeds that within dams. The size of the F value, although depending, in part, on the number of individuals within families, is an approximate measure of the relative part played by maternal inheritance in each flock.

TABLE 5.—MEAN PRODUCTION AND F VALUES FOR EACH OF THE SEVEN FARMS

Farm	Charlotte-town	Kent-ville	Nappan	Freder-icton	C.E.F. 1931	C.E.F. 1932	Harrow
Mean production	210.1	178.0	202.6	221.6	182.3	180.2	222.1
F value	1.58	2.68	1.67	0.71	1.69	1.79	0.97

It can be seen from the table that the order of the farms with regard to the mean production is the inverse of that with regard to the F values. In other words, the more favourable the environment and the more nearly

the birds reach the peak of their producing ability, the more nearly alike are the families and the harder it becomes to distinguish heritable differences.

While this relationship may be entirely fortuitous, it seems almost too consistent to be so. The correlation coefficient between the mean and F values is -0.847, the 5% and 1% points being 0.707 and 0.834 respectively. Such an unexpected relationship of heredity and environment might be explained by the existence of genes which interact with specific environments and which in the first paper of this series (3) were referred to as "protective" genes. Under this hypothesis, the superiority of certain individuals or families in flocks where the environment is sub-optimum and the average production therefore low, is due to the possession of "protective" genes which ward off, or overcome at least partially, the effect of these sub-optimum conditions on egg production. Conversely, the inferior egg producing families possess none or less than their share of "protective" genes.

This would explain the greater comparative effect of genetics in the poorer producing flock but also introduces a question which is of extreme practical importance. If the main genetic differences between families are due to"protective" genes, selection will be efficient only when the sub-optimum conditions prevail from year to year. Furthermore, if these protective genes are specific, *i.e.*, if they come into play only under specific sub-optimum conditions, then not only must sub-optimum conditions prevail from year to year but they must be qualitatively static or selection will be ineffective.

While it is possible that the sub-optimum conditions prevailing at any one farm, such as partial deficiency of a certain nutritive essential, may remain static from year to year, it is far more likely that conditions change, and that other conditions which depress egg production will exist the second year. This type of gene-environment interaction has been discussed by Munro (3). It is mentioned again here because the data in Table 5 are consistent with the existence of such an interaction, and because, if so, the F value of 1.47 in Table 3 may not be reflected in a positive dam-daughter correlation. In other words, while Table 3 shows that a small difference did exist between the transmitting ability of dams, it does not necessarily imply that the better laying dams produced the better laying daughters. The analysis thus far has shown only that the daughters from different dams are on the average slightly different in their egg producing potentialities. It indicates that selection of dams even on the basis of their daughters' production (*i.e.*, the progeny test) must be, at best, a laborious and inefficient method. This is confirmed by the work of Jull (2), who found very little relation between the mean egg production of daughters from the same dam mated to the same sire in each of two different years. There is an insignificant correlation coefficient of $+0.143$ between the eight pairs of means listed in Jull's Table 4.

DAM-DAUGHTER CORRELATION

Having inferred (Table 3) that maternal heredity was not entirely without effect, the next step was the estimation of how reliable the dam's record might be when used as an indicator of her daughters' production.

In other words, whether and to what extent selection on the basis of individual performance could be relied upon.

Jull (2) using data from Rhode Island Reds concluded that the number of eggs laid by the dam could not be used as a criterion of her breeding potentialities. Jull's conclusions were arrived at by comparing the mean of the mean egg production of daughters whose dams' records were above the mean egg production per dam for the pen (*i.e.*, the same sire) with that of the daughters whose dams' records were below the mean for the pen. His Table 2 shows thirteen pairs of means, the average difference in favour of the high dams being 1.076 eggs. When statistically analysed by the method for paired observations the t value amounts to only 0.249 which is very insignificant, the 5% point (I, Table 4) being 2.179.

In spite of the fact that all evidence having a bearing on the question indicated that very little if any correlation existed between a dam and her daughters, it was felt that a net correlation, secured by an analysis of covariance in which average differences due to sire and to location were removed might bring forth additional information. The pooled net correlation coefficient for all farms was found to be +0.152 while the corresponding regression coefficient was 0.153. Individual correlation and regression coefficients for each farm, and the coefficients obtained by pooling the variance and covariance within all farms, are shown in Table 6.

TABLE 6.—CORRELATION AND REGRESSION COEFFICIENTS SHOWING THE RELATION BETWEEN THE PRODUCTION OF A DAM AND MEAN PRODUCTION OF HER DAUGHTERS AT SEVEN FARMS, INDIVIDUALLY AND COLLECTIVELY

Farm	Value of r	Necessary value of r for P. of		Regression of daughters on dams
		0.05	0.01	
Charlottetown	0.179	0.345		0.145
Kentville	.310	.497		.274
Nappan	.162	.279		.153
Fredericton	−.054	−.367		−.049
C.E.F. 1931	.222	.361		.342
C.E.F. 1932	−.031	−.355		−.056
Harrow	.257	.355		.149
All farms	.152	.136	0.178	.153

The individual coefficients are all small and the statistical significance of the relation was established only by the method of pooling described above. That the relationship between the dam's production and that of her daughters is small, inconsistent and of very little or no practical importance is emphasized by the fact that two farms show very slight negative correlations. The data from Kentville show a correlation of +.31 which would be sufficiently high to assume practical importance providing it were a true measure of the actual relationship. This is by no means assured, however, since it is considerably less than the 0.05 error point and in view of the fact that the other farms exhibit much smaller correlations, it seems probable that chance has been largely responsible for much of the correlation in the Kentville data. The very small pooled

regression coefficient *viz.*, 0.153 shows that selection of dams on the basis of their trapnest record is not a practical procedure, even when these dams are mated to the same male and are housed and fed under uniform conditions. In actual practice, where dams are mated to different males and especially when they are housed and fed in different locations the effect of selection on the individual record will be even smaller than the above regression indicates.

DISCUSSION

The results presented in this paper are in substantial agreement with the tentative conclusions arrived at in the first two papers of this series. These may be briefly listed as follows: First, the majority of the variance which characterizes the yearly egg production records of a laying flock is caused by non-genetic factors. Second, increasing the egg producing potentialities of the domestic fowl by selective breeding is much more difficult than has been considered hitherto. This further implies that the increase which has occurred in egg production during the last fifteen or twenty years, in flocks where individual performance and pedigree has been largely relied on as the basis of selection, is in fact mostly due to improvements in feed and management.

A further point which should be kept in mind is the fact that the measurements used in this paper as indicators of the effect of heredity, *i.e.*, differences between dams and dam-daughter correlations, are not measurements. They have been freed of the effect of certain influences extraneous to the question under investigation by the statistical procedure adopted. These influences include average environmental differences between farms and years, the effect of the method of mating such as a tendency (deliberate or otherwise) to mate superior transmitting males to females which have already made high records, and spurious results arising from methods of grouping the data. It seems likely that much of the popular faith which has been placed upon the practice of mass selection by individual performance and pedigree arose from failure to recognize and isolate these extraneous influences.

SUMMARY

Data from the pedigree records of seven Dominion Experimental Farm flocks in eastern Canada have been assembled and analysed. This analysis revealed that under the experimental conditions maintained throughout these flocks:—

1. There was on the whole a slight difference between the transmitting ability of dams with regard to egg production. This difference did not attain statistical significance in small groups.

2. There was only a small and, for practical purposes, insignificant net correlation coefficient of +0.152 between the production of a dam and the mean production of her daughters. Individually, none of the seven farms showed a statistically significant correlation. The level of significance was attained only by pooling the variance and covariance within all farms.

3. The small size of the pooled net regression coefficient *viz.*, 0.153 shows that in flocks wherein females laying 200 or more eggs are used

exclusively as breeders, selection of dams on the basis of their trapnest record is not a practical procedure towards the segregation and concentration of high transmitting ability.

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Résumé

Transmission héréditaire de la ponte chez les volailles domestiques. III. Différences dans la capacité de transmission des mères, et degré de corrélation entre mère et fille. S. S. Munro, S. Bird et J. W. Hopkins, Ferme expérimentale fédérale et Laboratoires nationaux de recherches, Ottawa.

Les auteurs de cet article ont compilé et analysé les données relatives au pedigree de sept basses-cours des Fermes expérimentales dans l'Est du Canada. Cette analyse donne lieu aux constatations suivantes, dans les conditions expérimentales où se trouvaient ces basses-cours:—Il y a, tout considéré, en ce qui concerne la production des œufs, une légère différence entre les mères au point de vue de la capacité de transmission, mais cette différence est trop faible pour être exprimée par un chiffre en ce qui concerne les petits groupes. Entre la production d'une mère et la production moyenne de ses filles le coefficient net de corrélation n'était que de +.152, ce qui peut être négligé pour toutes fins pratiques. Prises séparément, aucune des sept fermes n'a révélé une corrélation significative. Ce n'est qu'en combinant ensemble les variations constatées sur toutes les fermes que l'on a pu obtenir une corrélation significative. Le peu d'importance du coefficient commun de régression, savoir .153, montre que dans les basses-cours où l'on se sert exclusivement pour la reproduction de femelles pondant 200 œufs ou plus, la sélection des mères sur la base de leur production contrôlée au nid-trappe n'est pas un moyen pratique tendant à la ségrégation et à la concentration d'une haute capacité de transmission.

INHERITANCE OF EGG PRODUCTION IN THE DOMESTIC FOWL

IV. RELIABILITY OF PROGENY TESTS OF SIRES

J. W. Hopkins[1], S. S. Munro[2] and S. Bird[2]

National Research Laboratories and Central Experimental Farm, Ottawa, Canada

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In the preceding paper of this series (4), the first-year egg-laying records of 1,165 individually pedigreed Barred Plymouth Rock pullets from seven Dominion Experimental Farm flocks in Eastern Canada were examined statistically. It was found that, on the whole, the variation in productivity between full-sisters was smaller than that between half-sisters by the same sire, and further that there was a slight tendency for the mean productivity of pullets derived from high-producing dams to exceed that of their half-sisters who were the daughters of below-average producers. The association between the number of eggs laid by the individual dams mated to each male and the mean number laid by their daughters in the succeeding season was however feeble, being represented by a correlation coefficient of only $+0.152$; and it was concluded that it would be impracticable to increase the productivity of these flocks by the selection of female breeders on the basis of their trap-nest record.

This circumstance provided further support for the earlier contention of Munro (3) that genetical improvement should be sought through the male parent. It is therefore the object of the present paper to put forward a few considerations of a statistical nature respecting the reliability of the progeny test as an index of the breeding potentialities of individual sires.

GENERAL CONSIDERATIONS

Suppose that a moderate number of pullets, sired by the same male, are reared together under specified conditions of management and nutrition, and trap-nested during their first year of laying, with the result that the average production is 230 eggs per bird. Is there any reasonable certainty that if this male was subsequently extensively employed as a breeder, the average egg-laying ability of his numerous daughters would not fall below a set standard of, say, 200 eggs per annum?

Suppose further that a second group of pullets, sired by a second male, but reared and tested together with the foregoing, have an average production of 250 eggs. Is it legitimate to infer that the second male is in fact genetically superior to the first?

From the statistical point of view, the actual pullets tested are to be regarded as a random sample of the infinitude of progeny which might conceivably have been generated by each male. The egg-laying ability of individual offspring will not in general be identical, but will be distributed about an (unknown) mean value. Similarly, the average of the relatively small group of progeny tested may be expected to deviate by a greater or lesser amount from the true but unknown general mean of which it provides an estimate. In order to pronounce upon the reliability

[1] Division of Biology and Agriculture, National Research Laboratories, Ottawa.
[2] Poultry Division, Central Experimental Farm, Ottawa.

or precision of the averages obtained in practice, or upon the significance of differences between such averages, numerical estimates of the random sampling variation to which they are subject are required.

The deviations to be expected in the averages will depend upon the nature and magnitude of the variation displayed by the individual progeny. With respect to the nature of such variation, studies of contest populations of the Barred Plymouth Rock breed by Munro (3) indicate that although the frequency distribution of individual differences does not follow the normal law exactly, the approximation to normality is close enough to permit the application of "normal" tests of significance to the averages (1, 5). The magnitude of the variations which may be expected to accrue from various sources is considered below.

EVALUATION OF SIRES AT A SINGLE FARM DURING THE SAME SEASON

In this case it is assumed that the offspring of all males tested have been subject to the same conditions of feeding, management and environment. The uncertainty attaching to the progeny averages under these particular conditions will then arise from two sources: (i) Variation between full-sisters, affecting the accuracy of the results from each mating, and (ii) differences between the true averages of different matings by the same male (*i.e.*, genetical differences between dams). Consequently, if the variance within full-sister families is assumed to be independent of the mean, the variance V_1 of the progeny average of any male, computed from the unweighted averages of full-sister families, will be

$$V_1 = \frac{1}{N^2} \overset{N}{\underset{1}{S}} \left(\sigma_d^2 + \frac{\sigma_s^2}{n_d} \right)$$

where N represents the number of dams whose daughters enter into the average, n_d ($d = 1, 2, \ldots, N$) the number of daughters from each dam, σ_s^2 the variance between individual full-sisters, and σ_d^2 the variance of the means of full-sisters.

Referring to Table 3 of the writers' previous paper (4), it will be seen that for the seven Experimental Farm flocks considered the estimated value of σ_s^2, based on 891 degrees of freedom, was 1496. Had all the 215 dams included been represented by an equal number n of daughters, the mean square of 2206 shown in the second line of this table would have provided a direct estimate of $\sigma_s^2 + n\sigma_d^2$. Actually however the numbers of daughters were not equal, so an approximate estimate of σ_d^2 was arrived at in the following manner. The mean square deviation between the unweighted means of full-sister groups was found to be 577, and the average number of pullets per group, 4.25. Roughly then

$$577 = \sigma_d^2 + \frac{1496}{4.25}$$

$$\sigma_d^2 = 225$$

and

$$V_1 = \frac{1}{N^2} \overset{N}{\underset{1}{S}} \left(225 + \frac{1496}{n_d} \right) .$$

In the event of each dam having an equal number of daughters this becomes simply

$$V = \frac{1}{N}\left(225 + \frac{1496}{n}\right).$$

The lowest value of V_1 for a specified total number Nn of pullets would therefore result from testing one daughter from each of Nn separate dams. Since such a test is not likely to be made in practice it is fortunate that the major variance is that between full sisters. As a result, when the total number of individuals is moderate, an appreciable reduction in V_1 may still be obtained by increasing the number of pullets per dam tested.

If instead of the unweighted mean, the weighted mean (*i.e.* the average of all pullets irrespective of dam) is employed when the numbers of full sisters are unequal, the variance V_2 of this quantity will be

$$V_2 = \frac{1}{[S(n_d)]^2} \sum_{1}^{N} \left\{ n_d^2 \left(225 + \frac{1496}{n_d}\right) \right\}.$$

and, owing to the preponderant effect of σ_s^2, this will in general be lower than V_1.

If the foregoing estimates of σ_d^2 and σ_s^2 are accepted as being generally applicable, the quantities V_1 and V_2 calculated from them may be used to compute: A, the amount by which the average of the daughters of a sire must exceed any set standard in order for the sire to be reasonably rated as superior to that standard; and B, the difference between the progeny of two males necessary in order that they may plausibly be regarded as differing in breeding worth.

In case A, suppose the standard to be set at 200 eggs. If now the male under consideration was in fact only of this calibre, nevertheless approximately 50% of his daughters must be expected to exceed this level of performance as the result of random variation. Similarly, the mean production of approximately 50% of the infinitude of possible sets of progeny of any specified size (from which the set of daughters actually tested is to be regarded as a single random selection) will likewise exceed 200. The probability of large deviations from 200 will however be less than that of smaller ones, and in particular, assuming approximately normal variation, 90% of all possible deviations may be expected to fall within the range $200 \pm 1.65\sqrt{V}$, and 5% to exceed $200 + 1.65\sqrt{V}$. Hence if only those sires whose test progeny exceeded this level were accepted, the chance of rating as superior a male which did not in fact exceed the standard would not exceed 1 in 20. By increasing the necessary difference, the probability of erroneous selection could be reduced indefinitely, but only at the cost of rejecting an increasing proportion of truly superior individuals.

Table 1 shows the necessary differences, $1.65\sqrt{V}$, computed from the foregoing estimates of σ_d^2 and σ_s^2, for the mean of n pullets from each of N dams. This illustrates the way in which V is reduced by increasing N and n. The table may also be used to make approximate tests of significance when the n_d do not differ greatly.

TABLE 1.—AVERAGE NUMBER OF EGGS LAID BY THE DAUGHTERS OF A SIRE IN EXCESS OF A SET STANDARD NECESSARY FOR A 5% LEVEL OF SIGNIFICANCE, COMPUTED FROM THE VARIANCE WITHIN FARMS AND SEASONS

No. of dams	No. of daughters per dam										
	2	3	4	5	6	7	8	9	10	11	12
2	36	31	28	27	25	24	24	23	23	22	22
3	30	26	23	22	21	20	19	19	18	18	18
4	26	23	20	19	18	17	17	16	16	16	15
5	23	20	18	17	16	15	15	15	14	14	14
6	21	18	16	15	15	14	14	13	13	13	13
7	19	17	15	14	14	13	13	12	12	12	12
8	18	16	14	13	13	12	12	12	11	11	11
9	17	15	13	13	12	11	11	11	11	10	10
10	16	14	13	12	11	11	11	10	10	10	10
11	15	13	12	11	11	10	11	10	10	9	9
12	15	13	12	11	10	10	10	9	9	9	9
13	14	12	11	10	10	10	9	9	9	9	9
14	14	12	11	10	10	9	9	9	8	8	8

In case *B* it is required to test whether an observed difference in the average number of eggs laid by the daughters of two sires may be reasonably taken as indicative of underlying genetical disparity.

If the sires were in fact similar, random differences between samples of their progeny would be expected to be distributed about zero with a standard deviation of $\sqrt{V_{m1} + V_{m2}}$, V_{m1} and V_{m2} being the variances appropriate to the progeny-averages of the two males. Assuming normal variation again, the difference necessary to reduce the frequency of erroneous distinctions to 5% will be $1.96\sqrt{V_{m1} + V_{m2}}$. On the other hand if the point at issue is not whether there is any difference at all between the two sires, but whether one particular individual, specified beforehand, is superior to the other, deviations from zero in one direction only are under consideration, and the 5% point will be at $1.65\sqrt{V_{m1} + V_{m2}}$.

EFFECT OF LOCALITY AND SEASON ON COMPARABILITY OF TESTS

The tests of significance outlined in the preceding section are restricted in their application to progeny tests made at a given place during the same season. It is desirable therefore to have an estimate of the additional variability affecting more general comparisons.

In order to secure some information on this point, recourse was again had to the annual egg-laying contest records previously utilized in another connection (3). Table 2 shows the average number of eggs laid by the Barred Plymouth Rock pullets in six different years in each of eight such contests. The total variance of these 48 quantities from their general mean was subdivided as shown in Table 3 into a portion due to average differences over all years, between farms, a second portion due to average differences, over all farms, between years, and a third portion due to irregular inter-annual and inter-farm variations. (2, Chap. VII).

Although the average number of eggs laid differed appreciably from farm to farm in the same year, and from year to year at the same farm, there was no consistent difference between farms or between years. Consequently, the mean square obtained from the total 47 degrees of freedom

TABLE 2.—MEAN YEARLY EGG PRODUCTION OF BARRED PLYMOUTH ROCK PULLETS BY CONTESTS FOR SIX YEARS

Year	Canadian (Ottawa)	P.E.I. (Charlottetown)	Nova Scotia (Nappan)	New Brunswick (Fredericton)	Quebec (Ste. Anne)	Quebec (Lennoxville)	Manitoba (Brandon)	Alberta (Lethbridge)	Yearly average
1926–1927	180.5	167.7	188.3	200.7	178.1	198.0	185.8	188.3	185.9
1927–1928	184.5	171.5	195.3	207.8	182.6	225.5	189.0	173.8	191.3
1928–1929	191.8	198.1	171.7	204.3	198.3	188.5	202.2	171.9	190.9
1929–1930	190.7	183.3	203.2	209.5	176.0	199.3	183.4	189.9	191.9
1930–1931	168.8	197.2	194.5	211.0	197.1	190.0	191.7	210.4	195.1
1931–1932	189.4	222.8	200.1	184.7	202.1	187.4	196.0	178.8	195.2
Contest average	184.3	190.1	192.2	203.0	189.0	198.1	191.4	185.5	191.7

TABLE 3.—ANALYSIS OF VARIANCE OF AVERAGE NUMBER OF EGGS LAID BY BARRED PLYMOUTH ROCK PULLETS IN ANNUAL CONTESTS

Variance due to	Degrees of freedom	Sum of squares	Mean square
Average differences between farms	7	1632.8	233.3
Average differences between years	5	462.3	92.5
Remainder	35	6047.0	172.8
Total	47	8142.1	173.2

may be used as an estimate of the variability in production arising from environmental differences. However, a portion of this mean square must have accrued from the random variance of individuals within contests, which was found to be 2031. As the average number of pullets per contest was 114, it will be more accurate to take 173 − 2031/114, or 155, as an extimate of σ_e^2, the environmental variance.

If now we wish to decide whether it is likely that a male under test is superior to a set standard not only under the particular conditions prevailing during the test, but in general, the necessary difference for a 5% level of significance will be $1.65\sqrt{V'_1}$ in the case of unweighted means of full-sister families, and $1.65\sqrt{V'_2}$ if account is taken of the number of full-sisters per family; where

$$V'_1 = \sigma_e^2 + \frac{1}{N^2} \sum_1^N \left(\sigma_d^2 + \frac{\sigma_s^2}{n_d} \right)$$

and

$$V'_2 = \sigma_e^2 + \frac{1}{[S(n_d)]^2} \sum_1^N \left\{ n_d^2 \left(\sigma_d^2 + \frac{\sigma_s^2}{n_d} \right) \right\} \quad (d = 1,2, \ldots, N)$$

again assuming that the mean and variance are independent.

Table 4, which is similar in form to Table 1, shows $1.65\sqrt{V'_{m1} + V'_{m2}}$, the necessary difference for a 5% level of significance, for various combinations of N and n.

It may be observed that the disparity between corresponding entries in Tables 1 and 4 is most pronounced when the number of daughters tested is large. By increasing the number of dams to which each sire is mated, and the number of daughters per dam tested, the evaluation of sires under the particular conditions prevailing at one farm during a single season might be effected with considerable precision; but this would not lead to any corresponding reduction in the environmental variance affecting other comparisons. The latter might be reduced either by testing each sire for more than one season at the same farm, or at more than one farm during the same season (by artificial insemination). Both of these methods are subject to obvious practical limitations.

The estimation of σ_e^2 also enables comparisons to be made of two males not tested at the same farm or in the same season. As already

TABLE 4.—AVERAGE NUMBER OF EGGS LAID BY THE DAUGHTERS OF A SIRE IN EXCESS OF A SET STANDARD NECESSARY FOR A 5% LEVEL OF SIGNIFICANCE, COMPUTED FROM THE VARIANCE WITHIN AND BETWEEN YEARS AND STATIONS

No. of dams	No. of daughters per dam										
	2	3	4	5	6	7	8	9	10	11	12
2	42	37	35	34	33	32	31	31	30	30	30
3	36	33	31	30	29	29	28	28	28	27	27
4	33	30	29	28	27	27	26	26	26	26	26
5	31	29	27	27	26	26	25	25	25	25	25
6	29	27	26	26	25	25	25	24	24	24	24
7	28	26	26	25	25	24	24	24	24	24	24
8	27	26	25	24	24	24	24	24	23	23	23
9	27	25	25	24	24	24	23	23	23	23	23
10	26	25	24	24	23	23	23	23	23	23	23
11	26	24	24	23	23	23	23	23	23	23	22
12	25	24	24	23	23	23	23	23	22	22	22
13	25	24	23	23	23	23	22	22	22	22	22
14	25	24	23	23	23	22	22	22	22	22	22

explained, the necessary difference in this case will be either $1.96\sqrt{V'_{m1}+V'_{m2}}$ or $1.65\sqrt{V'_{m1}+V'_{m2}}$, depending upon the nature of the comparison specified.

It will be understood that the foregoing estimates of variance and tests of significance are only approximate, furthermore that it is not known to what extent they apply to breeds other than the Barred Plymouth Rock. Nevertheless these calculations do provide some indication of the order of the uncertainty affecting the results of progeny tests in practice.

From the practical point of view, it may be pointed out that the usefulness of progeny testing will depend to a large extent on the standard adopted. In normal circumstances, this should be at least equal to the average production of the surviving birds within the farm, province or country in which the scheme is to be operated.

The single breeding plant, using limited numbers of males only, may expect to encounter the superior male but rarely. In order to concentrate the transmitting ability of such rare specimens intensive line or inbreeding must therefore be resorted to. This procedure, however, generally results in loss of vitality and reproductive ability.

A desirable alternative might be to bring together in a central breeding plant a number of males which had been proven to be superior by the procedures outlined above. These males could then be mated to foundation females in such a way that inbreeding was avoided.

Such a scheme could either be adopted as a co-operative enterprise by an organized breeders' association, or could be formulated and pursued as a national breeding policy by a government.

SUMMARY

Egg production records of pedigreed Barred Plymouth Rock pullets have been used to compute approximate numerical estimates of the random variation in the results of progeny tests of males arising from: (1) differences in productivity of full sisters; (2) differences between the average

productivity of the daughters of individual dams; and (3) differences in environmental conditions between locations and between seasons. These in turn have been combined to provide expressions for the estimated error variance of progeny tests comprising any number of dams and daughters, and for the necessary differences for significance in comparisons made under the same or different environmental conditions.

Some practical implications of the results obtained are briefly indicated.

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Résumé

Transmission héréditaire de la ponte chez les volailles domestiques. IV. A quel point peut-on se fier au contrôle de la progéniture des reproducteurs? J. W. Hopkins, S. S. Munro et S. Bird, Laboratoires nationaux de recherches et Ferme expérimentale centrale, Ottawa.

On s'est servi des relevés de ponte de poulettes pedigree Plymouths Rocks Barrées pour computer des évaluations numériques approximatives des variations constatées dans les résultats du contrôle de la progéniture des mâles et qui proviennent des suivants: (i) différence dans la productivité des sœurs; (ii) différences dans la productivité moyenne des filles de différentes mères; et (iii) différences dans les conditions de milieu entre endroits et saisons. On a combiné ensuite ces différences pour pouvoir exprimer les variations dans le contrôle de la progéniture portant sur un nombre quelconque de filles et de mères, ainsi que pour établir les différences nécessaires dans les comparaisons faites dans les mêmes conditions environnantes ou dans des conditions différentes. Quelques applications pratiques des résultats obtenus sont sommairement indiquées.